GROUP SIZE IN WEDGE-CAPPED CAPUCHIN MONKEYS (<u>Cebus</u> <u>olivaceus</u>):
VULNERABILITY TO PREDATORS,
INTRAGROUP AND INTERGROUP FEEDING COMPETITION

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1987

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Abstract of Dissertation Presented to the Graduate School
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May, 1987

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Most primates live in social groups. Do primates in social

groups benefit from increased feeding advantages or reduced

vulnerability to predators? This study addressed these

questions.

Wedge-capped capuchin monkeys, Cebus olivaceus, which occur

in the llanos of Venezuela, are ideal subjects for studies of the

advantages of group living in primates. The animals live in

groups that range in size from five to more than 40 animals.

Group ranges overlap completely. The abundance of their

resources varies spatially and seasonally. This monkey

population has been the subject of a long-term study since 1977.

Two groups of C. olivaceus were studied for a 17 month

period from May to July 1982 and from May 1983 to June 1984. One

group (26-36 animals) was about three times as large as the other (9-5 animals).

Intragroup feeding competition was more evident in large groups than in small groups. Animals were more spread out vertically. Agonistic interactions were more frequent. Animals spent less time feeding on fruit resources. Large groups moved farther, had an ongoing movement pattern, backtracked less, and used a larger area. However, the interpretation of these differences was difficult because animals in the two groups used different resources.

Seasonal comparisons indicated that feeding competition occurred in both groups. During periods of food scarcity, animals in both groups shifted from clumped food sources (fruit) to more evenly distributed food sources (insects), thus alleviating the effect of intragroup feeding competition.

Animals in large groups spent less time in vigilance and more time on the ground. These results are consistent with expectations based on decreased vulnerability to predators in large groups.

There is also among-group variation in foraging success. Large groups displace smaller groups, altering the use of time, movements, and use of space of these groups. Large groups have access to more resources, and are able to monopolize rare, spatially restricted food sources.

Most primates live in social groups of various sizes. There
are solitary animals such as lorises, monogamous groups such as
gibbons and siamangs, and multifemale groups such as baboons,
macaques and capuchin monkeys. There are two general ecological
hypotheses that address the question of why most primates live in
social groups. One suggests that animals in groups have foraging
advantages. The other is that group living animals are less
vulnerable to predators. The first has been championed recently
by Wrangham (1980), who has argued that animals living in groups
will have feeding advantages relative to solitary animals. The
second has been championed by van Schaik (1983), who proposed
that predator vulnerability is the primary factor encouraging
living in groups. Van Schaik also pointed out that social
animals will have to cope with higher intragroup feeding
competition and as a result, animals in groups will have a lower
feeding efficiency than solitary animals.

Wedge-capped capuchin monkeys, Cebus olivaceus
(=nigrivittatus, following Honacki et al., 1982) were used to
test the two hypotheses outlined above. First I review the
literature on group size in primates and the factors affecting
group size in social animals in general. The two hypotheses

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proposed by Wrangham (1980) and van Schaik (1983) are discussed and a number of predictions based on these hypotheses are tested. Lastly, the characteristics of C. olivaceus that make this species ideal for a test of these hypotheses are presented.

Group Size in Primates

Most primates live in social groups of different sizes (Jolly, 1985; Chalmers, 1980; Terborgh, 1983). Species that live in large groups tend to be found in more open areas, while forest living primates seem to live in smaller groups (Crook and Gartlan, 1966; Crook, 1970; Eisenberg et al., 1972). Within a species, group size is often smaller at lower population densities (examples, Table 1-1). When population size decreases, group size also decreases. This has been found in yellow baboons, Papio cynocephalus, vervet monkeys, Cercopithecus aethiops, and Toque macaques, Macaca sinica (Table 1-1), but not in Hanuman langurs, Presbytis entellus (Table 1-1).

Early workers suggested that particular group sizes were typical for a given species (Carpenter, 1942, 1954; Crook and Gartlan, 1966). More recent work has indicated that there is considerable intraspecific variation in group size, both in different areas (e.g., baboon, DeVore and Hall, 1965; howler monkey, Eisenberg, 1979b) and at specific sites (e.g., baboon, Altmann and Altmann, 1970). This variation has been examined statistically by van Schaik (1983). Van Schaik found that in interspecific comparisons, variation (measured using coefficient of variation) in group size increased with mean group size. The

TABLE 1-1

POPULATION DENSITY AND INTRASPECIFIC VARIATION IN GROUP SIZE IN SELECTED SPECIES

Species	Spacing system	Number of groups in study	Population density	Mean group size	Coefficient of variation in group size (%)
Papio cynocephalus	Overlap	51	2600(1)	50.8	59.57
		7	200(1)	30.8	64.98
Cercopithecus aethiops	Non-overlap	5	113(1)	22.6	54.60
		5	83(1)	13.0	28.30
Presbytis entellus	Non-overlap	26	24(2)	14.9	31.83
		14	13(2)	16.6	48.10
Macaca sinica	Overlap	17	346(1)	20.4	53.77
		17	293(1)	17.2	56.80

(1) Total population.
(2) animals per sq.km.
(3) References for P. cynocephalus are from Altmann and Altmann (1970) and Hausfater (1975), for C. aethiops are from Struhsaker (1976), for P. entellus are from Sugiyama and Parthasarathy (1978) and for M. sinica are from Dittus (1977).

interpretation of this result remains unclear, however, because
high variation in group sizes tended to be found in certain
genera, e.g., Macaca and Papio (van Schaik, 1983; Jolly, 1985;
Caldecott, 1986). Variation in group size might be more
pronounced in these genera, or it might be purely a consequence
of the number of studies on these genera.

Great variation in group size may also be found in species
that occur in a range of different habitats (Eisenberg et al.,
1972) e.g., baboons and macaques. Some species (e.g. Propithecus
verreauxi or white sifaka) however, seem to be able to adapt to
many kinds of habitats, without any associated variation in group
size (Richard, 1974, 1978).

The variation in group size may be larger when average group
size decreases (Table 1-1) but seems to be independent of the
spacing system reported for the species (Table 1-1; van Schaik,
1983). However, this trend is not universal (see the vervet
monkey, C. aethiops; Table 1-1).

Factors Affecting Group Size in Social Animals

Most primates are social animals. Group size in social
animals may be a result of (1) selection directly on group size
(Rodman, 1981; Brown, 1982; Terborgh, 1983; Pulliam and Caraco,
1984). Alternatively, group size may be a consequence of
selection on other traits (Lewontin, 1970, 1977, 1979; Gould,
1982; Gould and Lewontin, 1979), such as (2) simple demographic
processes: birth, immigration, death and emigration (Cohen,

1969, 1975) or (3) individual ontogenetic trajectories (Wiley, 1981).

Arguments that group size is an adaptive trait (Rodman, 1981; Brown, 1982; Terborgh, 1983; Pulliam and Caraco, 1984; Sibly, 1983; Giraldeau and Gillis, 1985) generally assume that an individual's inclusive fitness varies as a function of the size of the group in which that individual is found. An animal may benefit directly from group living through an increased ability to find or monopolize food (Eisenberg et al., 1972; Wilson, 1975; Clutton-Brock, 1974; Leighton and Leighton, 1982; Schoener, 1971; Wrangham, 1980) or by a reduced vulnerability to predators (Alexander, 1974; van Schaik, 1983; Terborgh, 1983). However, by living in groups, animals must cope with higher intragroup feeding competition (van Schaik, 1983; Janson, 1985; Watts, 1985). Group size may be set by an optimal trade-off between increased predator protection and decreased foraging opportunity (Terborg, 1983; Wilson, 1975).

Other authors argue that group size is a consequence of selection on other traits (e.g. Lewontin, 1970). Cohen (1969), for instance, proposed a model to account for the observed distribution of group sizes in wild primates. He proposed that group size is the result of selection on one or all of four main demographic processes: birth, immigration, death and emigration. The distributions predicted by his model matched the observed distribution of group sizes in a number of primates including gibbons (genus Hylobates), yellow baboons (Papio cynocephalus) and howler monkeys (Alouatta palliata). These results suggest that natural selection may act directly on population parameters

and not on group size per se (Altmann and Altmann, 1979).
Alternatively, selection may act on individual ontogenetic
trajectories or individual schedules of social development
(Wiley, 1981), and group size is an indirect consequence of this
selection. Each individual animal changes its social status
according to its age or seniority and vacancies in the social
hierarchy. This model has successfully accounted for the
distribution of group sizes in the communally breeding stripe-
backed wren (Campylorhynchus nuchalis) (Wiley and Rabenold,
1984; Rabenold, 1985).

Group Living in Primates: Food or Predators?

Wrangham (1980) proposed that group size affects access to
patchily distributed resources. He argued that males and females
are subject to different evolutionary forces. Mate acquisition
is more important for the male, while food acquisition is more
important for the female. Females should track the distribution
of food while males should track the distribution of females. If
resources are patchily distributed in space, and if large groups
of females are able to displace small groups from resources, then
female kin should tend to stay together and form long-term
relationships. The result is the "female-bonded group".

Wrangham (1980) did not reject reduced vulnerability to
predators as a benefit of social living, but he viewed it as less
important than intergroup feeding competition. Wrangham (1980)
also accepted that there is a cost to living in a group because
of intragroup feeding competition. However, he regarded this

cost as compensated by benefits obtained from success in intergroup feeding competition. Wrangham noted that there are two possible responses to food scarcity within such a group. As females in the female-bonded group are mostly kin and intragroup feeding competition should be most intense during periods of food scarcity, females should either emigrate to reduce the cost to their kin, or they should switch from high to low quality food.

On the other hand, van Schaik and van Hooff (1983) and van Schaik (1983) proposed the alternative view that predator avoidance is the primary cause of group-living in primates. Van Schaik proposed that living in a group always carries the cost of high intragroup feeding competition. Large groups will therefore have lower feeding efficiencies, and this cost must be balanced by the benefit of reduced predator vulnerability. This hypothesis ignores any benefit of intergroup feeding advantage. Van Schaik's (1983) hypothesis also does not address the effect of season on the use of time, space and resources. No matter what the season is, he predicted that intragroup feeding competition will be higher in the large group than in the small one.

Van Schaik (1983) predicted that (i) larger groups should be better at detecting predators and (ii) in forest primates, small groups should spend more time higher off the ground to avoid predators.

Cebus olivaceus: a Candidate for Testing
Wrangham (1980) and van Schaik (1983)'s Hypotheses

Wedge-capped or weeper capuchin monkeys (Cebus olivaceus) in the llanos of Venezuela demonstrate characteristics that are ideal to test the predictions derived from Wrangham (1980) and van Schaik (1983)'s hypotheses.

(1) They live in groups that range in size from five to more than 40 animals (Robinson, 1986; this study).

(2) They live in female-bonded groups, in which females tend to stay in their natal group while males emigrate (Robinson, in preparation).

(3) They inhabit a seasonal forest in which fruit trees are clumped (Robinson, 1986). This allows groups to defend discrete patches of food (Robinson, 1985). The availability of fruit and certain invertebrate prey also varies seasonally with a peak in the wet season (Robinson, 1986).

(4) Group ranges overlap completely (Robinson, 1986) and groups must compete directly for the same resources.

(5) Last, but most important, is that this monkey population has been well studied (Robinson, 1981, 1984a, 1986; Fragaszy, 1986; de Ruiter, in press) and basic information on ecology, behavior and demography are already available.

CHAPTER II
STUDY SITE AND METHODS

Study Site

The study site was Fundo Pecuario Masaguaral in the central
llanos of Venezuela, a cattle ranch owned by Sr. Tomas Blohm.
Its location is $8^{o} 34^{/}$ N and $67^{o} 35^{/}$ W, about 45 Km south of
Calabozo. The nearest village is Corozo Pando. It has been an
active site of wildlife research (e.g. Montgomery and Lubin,
1977; Eisenberg, ed., 1979a; Wiley and Wiley, 1980; Rabenold,
1985; Austad and Rabenold, 1985).

My study site was in the riparian gallery forest that
covered the eastern part of the ranch. This forest is bordered
by the Cano Caracal and the Rio Guarico. The forest can be
classified broadly as dry tropical forest (Ewel et al., 1976).
The annual rainfall is about 1450 mm and is highly seasonal with
most of the rain falling between May and October (Robinson,
1986).

Three broad types of vegetation can be classified within the
forest according to soil types (Tayler, 1978; Robinson, 1986):
forests on loamy sand, loam, and clay soils, respectively.
Certain species of trees occur broadly in all forest types, e.g.,
the palm Copernicia tectorum and the guacimo Guazuma tomentosa.

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Others have a highly clumped distribution, e.g., the guarataro
Vitex orinocensis.

Most tree species in this forest are patchily distributed in
space, and bear fruit in a very seasonal manner (Robinson, 1986).
More species fruit during the rainy than the dry season. The
fruit availability therefore is highly patchy in both space and
time. A detailed description of the study site appears in
Robinson (1986). The descriptions of the forests in general in
this llanos region can be seen in Monasterio and Sarmiento
(1976), Troth (1979), and Sarmiento (1984).

Study Animals

The study animals are wedge-capped capuchin monkeys, Cebus
olivaceus (=nigrivittatus following Honacki et al., 1982). This
is a New World primate belonging to the family Cebidae (Jolly,
1985). This species is distributed from the Orinoco River basin
to the northern bank of the lower Amazon and Negro Rivers (Freese
and Oppenheimer, 1981).

The study population on this ranch was studied very briefly
by Oppenheimer and Oppenheimer (1973) in 1969. Robinson started
long-term research in 1977. Researchers working with this
population include Robinson (1981, 1984a, 1986), Fragaszy (1986)
and de Ruiter (in press). This study is a part of a long-term
study on demography and social organization of this species.

About 14 groups were contacted during the study period
(Table 2-1). Group sizes and composition within the study area
changed little between Robinson's and my study period.

TABLE 2-1

GROUP SIZES AND COMPOSITION OF WEDGE-CAPPED CAPUCHIN MONKEYS

Group	Adult male	Adult female	Subadult male	Juvenile male	Juvenile female	Juvenile unknown	Infant	Total	Source or last day of census
Blue	1	5	2	2	2	1	2	15	January 7 1984
Brown	1	2	2	2	1	1	1	10	June 4 1984
Chestnut	1	+4	+1	+2	0	0	+2	+15	Robinson, pers. comm.
Cinnamon	1	+8	4	+3	+3	0	+2	+40	Robinson, pers. comm.
Coco	1	7	1	4	0	0	1	14	Robinson, pers. comm.
Grey	1	7	3	1	6	0	1	19	Robinson, pers. comm.
Main	1	9	4	4	5	2	1	26	May 16 1982
Main	1	11	5	4	7	5	3	36	June 29 1984
Newcoco	1	2	3	1	0	1	1	9	May 5 1984
Northern	2	+6	+3	+4	+7	0	+2	+40	Robinson, pers. comm.
Orange	1	7	1	2	6	0	4	22	Robinson, pers. comm.
Oro	1	+2	3	1	0	1	1	+25	May 23 1984
Pale	1	4	2	1	3	2	1	14	June 4 1984
Pink	1	5	1	1	1	4	0	14	June 4 1984
Red	1	7	3	7	5	0	4	28	Robinson, pers. comm.
White	1	4	0	1	2	1	1	9	May 21 1982
White	1	1	0	2	0	1	0	5	July 22 1984

Most observations were concentrated on two groups, Main and White. Main group was studied intensively by Robinson (1977-1979), Fragazy (1980-1981) and de Ruiter (1981-1982) and I will call it the LARGE group. White group has been censused by Robinson since 1977 and was a subject of preliminary comparative behavioral study by de Ruiter (in press). I will call this group the SMALL group.

Both groups were habituated to me at the beginning of my study. Animals in both groups were individually recognized (see Figure 2-1) and my identifications were checked for accuracy in the field by Dr. Robinson and Mr. de Ruiter. The LARGE group increased in size from 26 to 36 while the SMALL group decreased in size from 9 to 5 during my study period. The changes in composition of the groups can be seen in Table 2-2 and 2-3. The LARGE group increased in size mostly as the result of births while the SMALL group decreased in size as the result of deaths of old animals.

Studies of primate ecology and behavior cope with special kinds of problems. Few studies of primate ecology and behavior include more than one group in comparable detail (Clutton-Brock, 1977). In this study, all inferences were based on one small and one large group. It is hardly possible for the study of this sort to follow the principles of experimental design suggested for ecological studies (see Hurlbert, 1984; Hawkins, 1986).

Figure 2-1. Example of individual monkeys in the SMALL
group. The following list is from the left to the right and from
the top to the bottom: (1) an adult male (Scar Lip, SL), (2) an
old adult female (Beret, BT), (3) an adult female (Furry Face,
FF), (4) an older juvenile male (Benno, BN), (5) an older
juvenile female (Geje, GE), (6) a young juvenile female (Irma,
IR), (7) younger juvenile female (Petra, PT) and (8) a very young
juvenile female (Frances, FR) sitting next to the large adult
male (SL).

TABLE 2-2

DEMOGRAPHIC CHANGES IN THE LARGE GROUP, 5 MAY 1982 - 29 JUNE 1984

Date	Change	Animal	New group size
9 July 82	Birth	F Penny (born to Pinnocchio)	27
		M IH (born to Hi)	28
11 July 82	Infanticide	IH (by Big Male)	27
25 July 82	Birth	F Puffy (born to Pointed Face)	28
21 May 83	Immigration	Subadult M Rudiger	29
23 May 83	Birth	F Hanna (born to Hi)	30
	Birth	M Bobo (born to Butte)	31
	Birth	M Angel (born to Amelia)	32
11 June 83	Birth	M Mana (born to Mary Francis)	33
27 June 83	Birth	F Malee (born to Mo)	34
19 May 84	Birth	? BE's infant (born to Becky)	35
29 June 84	Birth	? WH's infant (born to Whity)	36
		? CR's infant (born to Crawley)	37

F, M and ? stand for female, male and unknown sex, respectively

TABLE 2-3

DEMOGRAPHIC CHANGES IN THE SMALL GROUP, 21 MAY 1982 - 16 JUNE 1984

Date	Change	Animal	New group size
22 July 82	Birth	F France (born to Furry Face)	10
24 May 83	Death	Adult F Margaret	9
8 July 83	Immigration	Subadult M Charlie	10
10 Aug 83	Death	Adult F Bare Shoulder	9
29 Sept 83	Emigration	Subadult M Charlie	8
12 Nov 83	Death	Adult F Beret	7
1 Feb 84	Death?	Younger Juvenile F Petra	6
29 Feb 84	Emigration	Older Juvenile M Benno	5

F and M stand for female and male respectively

Methods

The observations were made from May to July 1982 and from
May 1983 to July 1984. Observation periods were paired, one with
the LARGE and the other with the SMALL group, so that results
could be compared. I minimized the interval between observation
periods as much as possible. In July 1982 I tried 5-day
continuous observations on each group, following a tradition of
primate field studies (e.g. Struhsaker, 1975). To reduce the
time between the paired observation periods with the LARGE and
the SMALL group, I reduced the observation period on each group
to 2 days in June 1983. The dates of systematic observation
periods during 1983-1984 can be seen in Figure 2-2.

Observations on other groups were made opportunistically.
Animals in each group were described by noting the unique
characteristics of individuals in each particular group. The
identity of groups was double-checked with Dr. Robinson during
his annual censusing period. The observations on other groups
also allowed me to examine relations among all groups in the
study area.

Figure 2-2.   Diagram showing 13 pairs of observation periods during 1983-1984.   The back and white blocks represent observations on the LARGE and SMALL groups respectively.

DATE
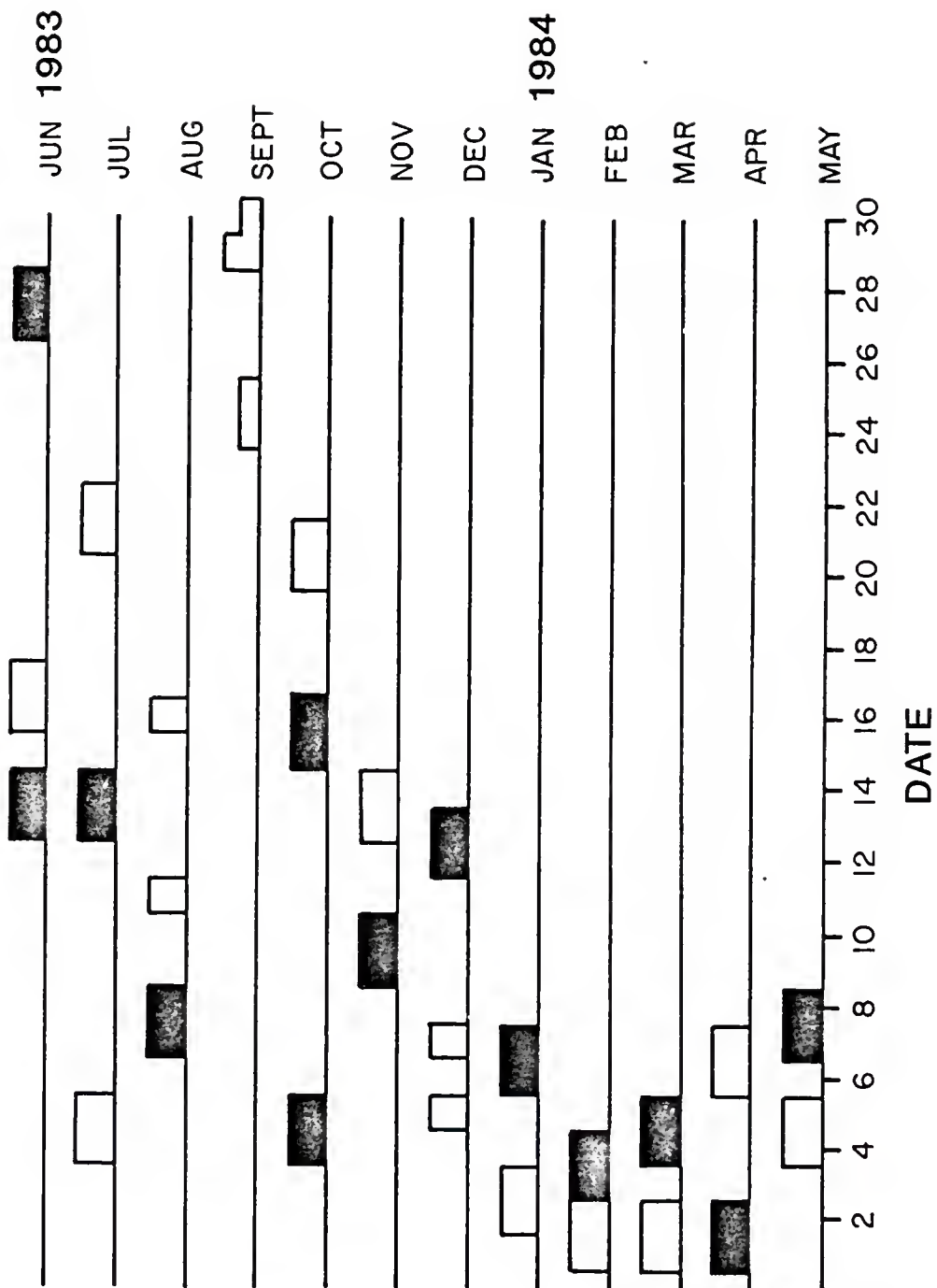
CHAPTER III
GROUP SIZE AND INTRAGROUP FEEDING COMPETITION

Introduction

Intragroup feeding competition was recognized as a
potentially important factor determining group living in primates
by both Wrangham (1980) and van Schaik (1983). Van Schaik (1983)
viewed it as a direct cost while Wrangham (1980) viewed it as a
side-effect of group living. Demonstration of higher intragroup
feeding competition in large groups will not support or reject
either hypothesis.

Two approaches will be used to test if there is intragroup
feeding competition among animals in groups. One approach is to
compare groups of different sizes. There should be higher
intragroup feeding competition in larger groups. This intragroup
feeding competition will affect the use of time, movement, use of
space and access to resources. The other approach is to compare
the same group at different seasons. There should be higher
intragroup feeding competition during the period of food
scarcity. To reduce this intragroup feeding competition, animals
should use lower-quality food with more homogeneous distribution
during the period of resource scarcity. These changes, in use of

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time and space, group movements, and use of resources, should be greater in large groups than small groups.

This chapter will demonstrate that there is higher intragroup feeding competition in large groups. The use of time and space in groups of different sizes and in the same groups at different seasons will be compared.

Methods

Sample Periods

During this study, I completed 16 paired observation periods. Three pairs were made in the summer of 1982 and the remainder in 1983-1984. Each pair lasted for two days in each group, except for two periods in summer 1982 in which five days of observations were made on each group.

The wet season use-of-time data were derived from six paired periods from June to November, 1983. The dry season data were derived from five paired observation periods from December 1983 to April 1984.

Observations on group movement and use of space were from the 14 paired sample periods. The sample periods for movement in the wet and dry seasons were the same as the observations on the use of time. For comparative reasons, the use of space was calculated from 5 observation periods in each season. They were from June to October 1983 in the wet season and December 1983 to April 1984 in the dry season.

Behavioral Sampling and Use of Time

Each systematic observation day (0600-1800) was divided into 24 half-hour sample periods for the LARGE group and 48 fifteen-minute periods for the SMALL group. Instantaneous samples of behavior (Altmann, 1974) were made on each individual, five seconds after the animal was first located in each sample period. No individual was sampled more than once in a sample period. Except for defining a "vigilance" category, I adopted the same categories of behavior used by Robinson (1986). These included nine broad categories: foraging, feeding, moving, resting, self cleaning, social grooming, playing, vigilance, and other social and non-social behavior. Foraging is defined as looking for and feeding on invertebrate prey. Feeding is defined as actually ingesting food and is virtually restricted to items of plant origin. The foraging category has more subcategories than any others (see details in Robinson, 1986). During foraging I recorded whether an item was ingested during the five seconds immediately following a record, and this allowed me to quantify capture success. Vigilance was defined as the activity when animals were alert and looking around but were not foraging or feeding.

All social interactions were also noted opportunistically using the ad libitum method (Altmann, 1974). In other words, I recorded all social interactions whenever they were noted. I paid special attention to aggressive interactions. Most aggressive interactions were associated with vocalizations (trills, whistles, screams) (Robinson, 1984b), making them easy to

detect. Some aggressive interactions that were not associated with loud vocalizations (e.g., open mouth threat, see also Oppenheimer, 1973; Klein, 1974; Weigel, 1978) might have been missed.

Movement and Use of Space

Before I began my study, an extensive trail system was established by Robinson, Fragaszy and de Ruiter. The trails were marked with colored plastic flags and marked aluminum tags every 25 meters. The trail system was approximately 60 km long. During my study period, I maintained this system and also extended trails to areas that were used by the SMALL group, mainly in the northern part of the study site (Figure 3-1).

Locations of the study groups were noted every half-hour starting at 0600 h until 1800 h on all systematic observation days. The center of mass of the group was carefully placed on the map. The center of mass of the group is defined as the approximated location of a center of a group.

To study group movements, two variables were measured from the observed group paths. These were half-hour movements and half-hour turning angles. Half-hour movements measure the distances from two centers of mass in consecutive half-hour periods. Half-hour turning angles measure angular deviations from straight ahead between consecutive half-hour movements. Both half-hour movement and turning angle have been used before in primate studies (Waser, 1976; Robinson, 1986).

Figure 3-1. Map of the study area showing trail system, rivers, and ranch boundaries.
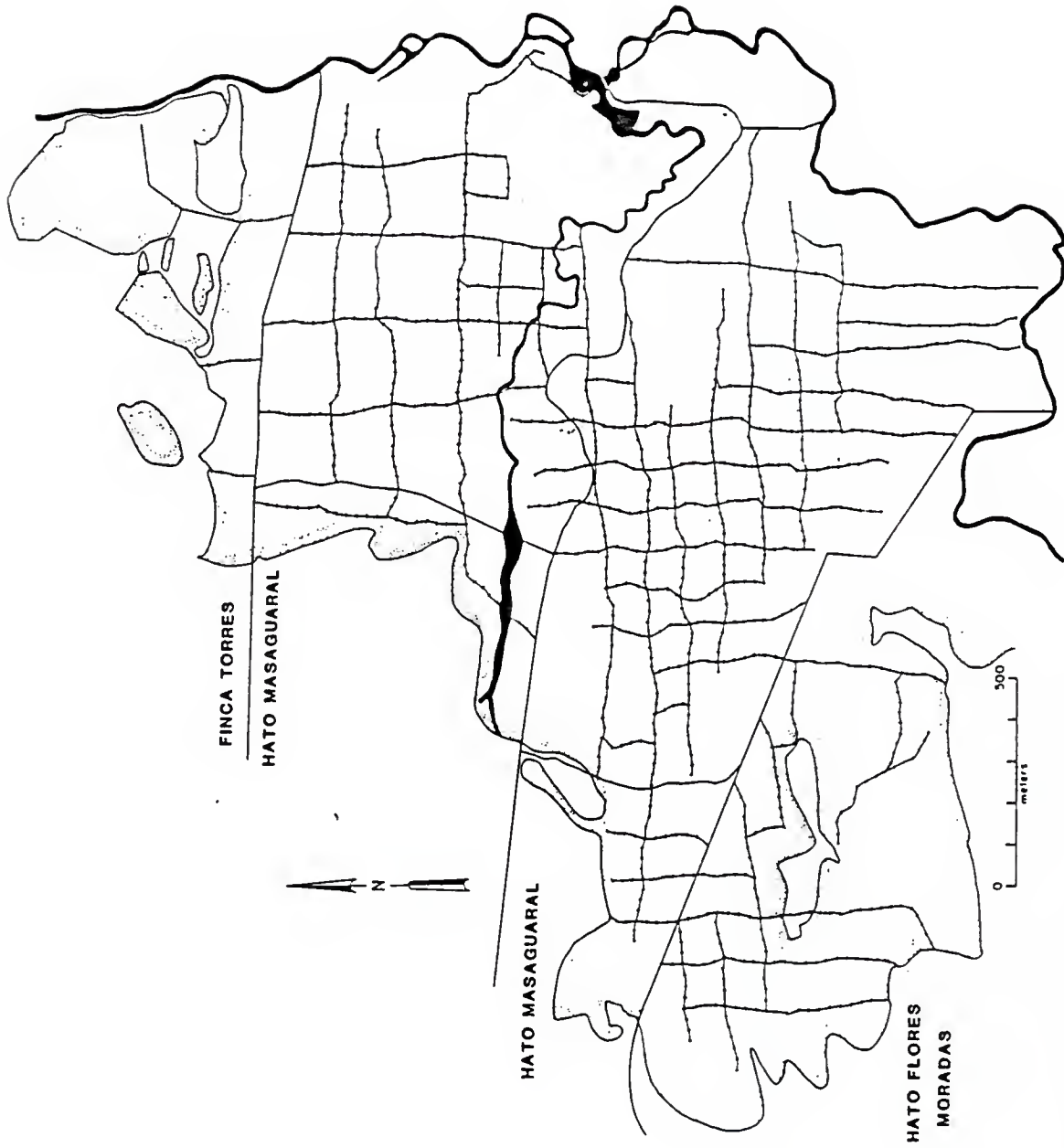
FINCA TORRES

HATO MASAGUARAL

N

HATO MASAGUARAL

HATO FLORES
MORADAS

0   500
meters

To study the use of space of the two groups, one-hectare quadrats were used. The quadrat locations and sizes are identical to those of Robinson (1986). Each half-hour location of the center of mass was considered as a single score when the use of area of the two groups was calculated. Home range was calculated by the total number of quadrats occupied during the half-hour locations in a specified period of time.

To study the vertical use of space of the group, the height above ground was noted every time a behavioral observation was made. The heights were lumped into 5 categories: ground (=0), 1-5, 6-10, 11-15, and 16-20 m from the ground. The lumped categories may reflect different foraging microhabitats.

Every time a behavioral observation was made, the distance and identity of nearest neighbors was noted whenever possible. The distance was estimated in 1 m intervals up to 10 m.

Use of Resources

During behavioral observations, I noted the object types in which animals were foraging. When the monkeys fed, the food was classified as to animal or plant origin.

Plant material used by the animals was identified by various methods. Most of the important plant species used by the animals were shown to me by Dr. Robinson at the beginning of my study. Some plants were identified and tagged. I also consulted the local people or resident botanists at the ranch. Three references which I used for plant identification were Ramia (1974), Hoyos (1979) and Steyermark and Huber (1978). Most

plants used by the monkeys were identified to species. In contrast, food of animal origin was rarely identified.

Data Analysis

Statistical analysis relied on SPSSx version 2.1 (SPSS, Inc., 1986). Most analyses used non-parametric statistics (Siegel, 1956) except where indicated. Use of parametric tests followed Sokal and Rohlf (1981). When non-parametric tests were used with a large set of data, a sample was randomly selected from the appropriate data using option 4 in SPSSx (SPSS, Inc., 1986).

To compare variation such as in vertical use of space, coefficients of variation were compared. The logarithm to the base 10 was also taken for each datum to estimate relative variability (Lewontin, 1966). This allowed me to use Kruskal-Wallis one-way ANOVA to test for significant differences (Sokal and Braumann, 1980).

Results

Intergroup Comparison

Effect on Spacing

Prediction 1: The higher intragroup feeding competition among animals in larger groups will affect individual feeding efficiency so in order to reduce intragroup feeding competition, animals in larger groups should spread themselves out more.

Nearest-neighbor-distances among animals should be greater in larger groups.

Nearest-neighbor-distances among animals in both large and small groups were comparable. The mean nearest-neighbor-distance among animals in the LARGE group was 3.8 m while in the SMALL group it was 3.9 m (Table 3-1), a difference that is not statistically significant (Mann-Whitney U-test, n_L =527 instantaneous samples, n_S =378 instantaneous samples, p>0.1).

Prediction 2: To reduce intragroup feeding competition, animals in large groups should spread themselves vertically more extensively. This may be because by spreading themselves vertically, animals in a group will use different microhabitat or different resources. Consequently, animals avoid intragroup feeding competition.

The vertical spread of the animals in the LARGE group was more extensive than that in the SMALL group. This is shown both by coefficients of variations and relative variabilities. The coefficient of variation in height for animals in the LARGE group was higher (69.8% in the LARGE group versus 44.1% in the SMALL group). The relative variabilities in height for animals in both groups was significantly different (Kruskal-Wallis one-way ANOVA, n_L =1929 instantaneous samples, n_S =1578 instantaneous samples, p<0.01).

TABLE 3-1

THE NEAREST NEIGHBOR DISTANCE (m) AMONG ANIMALS IN BOTH GROUPS

Group	Season	Mean	Median	SD	Total records
	Overall	3.8	4.0	2.31	2689
LARGE	Wet	3.6	3.0	2.44	478
	Dry	3.0	3.0	1.79	474
	Overall	3.9	4.0	2.35	2315
SMALL	Wet	3.9	4.0	2.26	692
	Dry	3.5	3.0	1.89	316

Effect on Social Interactions

Prediction 3: The higher intragroup feeding competition may be exhibited as a higher frequency of agonistic interactions. I expected that frequency of agonistic interaction would be greater in large groups.

The animals in the LARGE group interacted aggressively more frequently with one another than those in the SMALL group. The mean rate of agonistic interactions among animals in the LARGE group was 23.75 per day (n_L =8 days) while in the SMALL group it was 7.75 per day (n_S =8 days). This frequency of agonistic interactions was significantly different (t-test, 14df, p<0.01).

Note that because nearest-neighbor-distances did not differ significantly between the groups, this is not a consequence of more potential interactants being closer together in the LARGE group.

Effect on Time Budgets

Prediction 4: The higher intragroup feeding competition in larger groups should result in lower invertebrate foraging success. This is because the number of animals in large groups should reduce the invertebrate resource base and thereby reduce capture success. It is predicted that the animals in large groups should have lower invertebrate foraging success.

Overall, animals in both groups had equal capture success (13.6%, n_L =3449 instantaneous samples versus 12.5%, n_S =2547 instantaneous samples; chi-square test, 1df, p>0.1). This effect

was consistent across all microhabitats (Table 3-2; chi-square test, 1df, p<0.01 for all categories).

Prediction 5: The higher intragroup feeding competition should result in lower access of animals in a group to fruit resources. This may be the result of higher agonistic interactions in large groups or animals may avoid each other. I expected that the animals in large groups would spend less time feeding.

Table 3-3 shows how both groups used their time. The LARGE group spent less time feeding as predicted (chi-square test, 1df, p<0.01).

Prediction 6: If higher intragroup feeding competition results in less access to resources, then animals in larger groups should allocate more time to foraging (sensu latu) than animals in smaller groups. I expected that the animals in large groups would spend more time feeding, foraging and moving combined together.

Contrary to prediction, the animals in the LARGE group spent less time feeding, foraging and moving combined (73.3% versus 75.9%, Table 3-3) than animals in the SMALL group (chi-square test, 1df, p<0.01).

This result may be a consequence of animals in the two groups using different resources, or of animals in the LARGE group having higher priority of access to clumped and restricted resources (Chapter V).

TABLE 3-2

DIFFERENTIAL CAPTURE SUCCESS (%) IN DIFFERENT MICROHABITATS

| Category | Capture success (%) | | Total sample | |
	LARGE group	SMALL group	LARGE group	SMALL group
Dry twig	33.3	36.2	189	221
Dry branches	34.6	31.5	81	111
Leaves	50.8	36.8	59	117
Insects	67.3	62.9	52	35
Bark	20.0	21.0	40	62
Palm leaves	37.1	21.3	89	47
Palm nuts	21.5	20.0	330	50
Twigs	9.7	19.5	31	41
Dry palm leaves	23.7	16.3	59	43
Dry leaves	52.4	22.2	21	36
Palm boots	16.9	34.6	71	26
Leaf litter	2.4	0	206	32
Palm tops	20.0	13.6	25	22
Dry boughs	13.3	25.0	23	24
Palm branches	51.2	72.2	43	18
Branches	87.5	80.0	24	20

TABLE 3-3

TIME BUDGET (%) OF ANIMALS IN THE LARGE AND SMALL GROUP

	% Time	
	LARGE group	SMALL group
Forage	28.6	29.7
Feed	14.1	19.6
Rest	10.1	12.8
Move	30.6	26.6
Drink	0.9	0.4
Socialize	13.7	8.2
Non-socialize	1.0	1.2
Vigilance	0.9	1.5
Total instantaneous samples	13,630	9,419

Prediction 7: The higher intragroup feeding competition should allow less time for animals in larger groups to rest. This may be the result of animals in larger groups spending more time interacting agonistically or avoiding one another. I expected that animals in larger groups would spend less time resting.

The animals in the LARGE group spent less time resting (10.1% versus 12.8%, Table 3-3) than animals in the SMALL group (chi-square test, 1df, p<0.01).

Prediction 8: If animals in larger groups spend more time avoiding one another, then they should spend more time moving. I expected that animals in larger groups would allocate more time to moving.

The animals in the LARGE group spent more time moving (30.6% versus 26.6%, Table 3-3) than animals in the SMALL group (chi-square test, 1df, p<0.01).

Effect on Group Movement and Use of Space

Prediction 9: Avoiding intragroup feeding competition by moving should also result in more extensive group movements. I expected that larger groups would move farther than smaller groups.

The length of the day-range in the LARGE group was longer. The mean length of day-range in the LARGE group was 2,400 m (SD=506 m, n =29 days) while that of the SMALL was 2,000 m

L

(SD=468 m, n =24 days), a difference that was statistically
          S
significant (t-test, t=3.07, p<0.01).

The mean half-hour step length of the LARGE group was also
longer. The mean half-hour step length in the LARGE group was
99.8 m while that of the SMALL group was 81.7 m (Table 3-4), a
difference that was statistically significant (Mann-Whitney U-
test, n =734 records, n =725 records, p<0.01, Figure 3-2).
      L   S

Prediction 10: If animals in groups of different sizes used
the same resource base, then animals in larger groups should
exploit their resource faster. The disadvantages of turning
around and returning to previously occupied areas or previously
exploited fruit trees should be greater in larger groups. As a
result, larger groups should tend to move forwards more and
backtrack less than smaller groups. I predicted that half-hour
turning angles in larger groups would be smaller on average than
turning angles in smaller groups.

The mean half-hour turning angle of the LARGE group was
smaller than that of the SMALL group. In the LARGE group, it was
      o   o
50.9 while in the SMALL group it was 64.9 (Table 3-5), a
difference that was statistically significant (Mann-Whitney U-
test, z=-5.06, n =680 records, n =622 records, p<0.01). In
              L   S
addition, Figure 3-3 indicates that the overall distribution of
turning angles of the LARGE group is more skewed towards smaller
turning angles.

Another interpretation of this result is that the larger
half-hour turning angles of smaller groups is a consequence of

TABLE 3-4

THE HALF-HOUR STEP LENGTH (m) IN BOTH GROUPS

Group	Season	Mean	Median	SD	Total records
	Overall	99.8	84.0	67.91	734
LARGE	Wet	97.4	85.0	60.84	284
	Dry	90.2	73.0	68.33	234
	Overall	81.7	65.0	69.21	726
SMALL	Wet	85.8	65.0	72.29	284
	Dry	71.7	58.0	71.74	227

Figure 3-2. Distribution of distances moved in all half-hour periods (step-lengths) in both groups. The continuous and broken lines represent the Maxwellian distribution (Waser, 1976) with and without zero distances respectively.
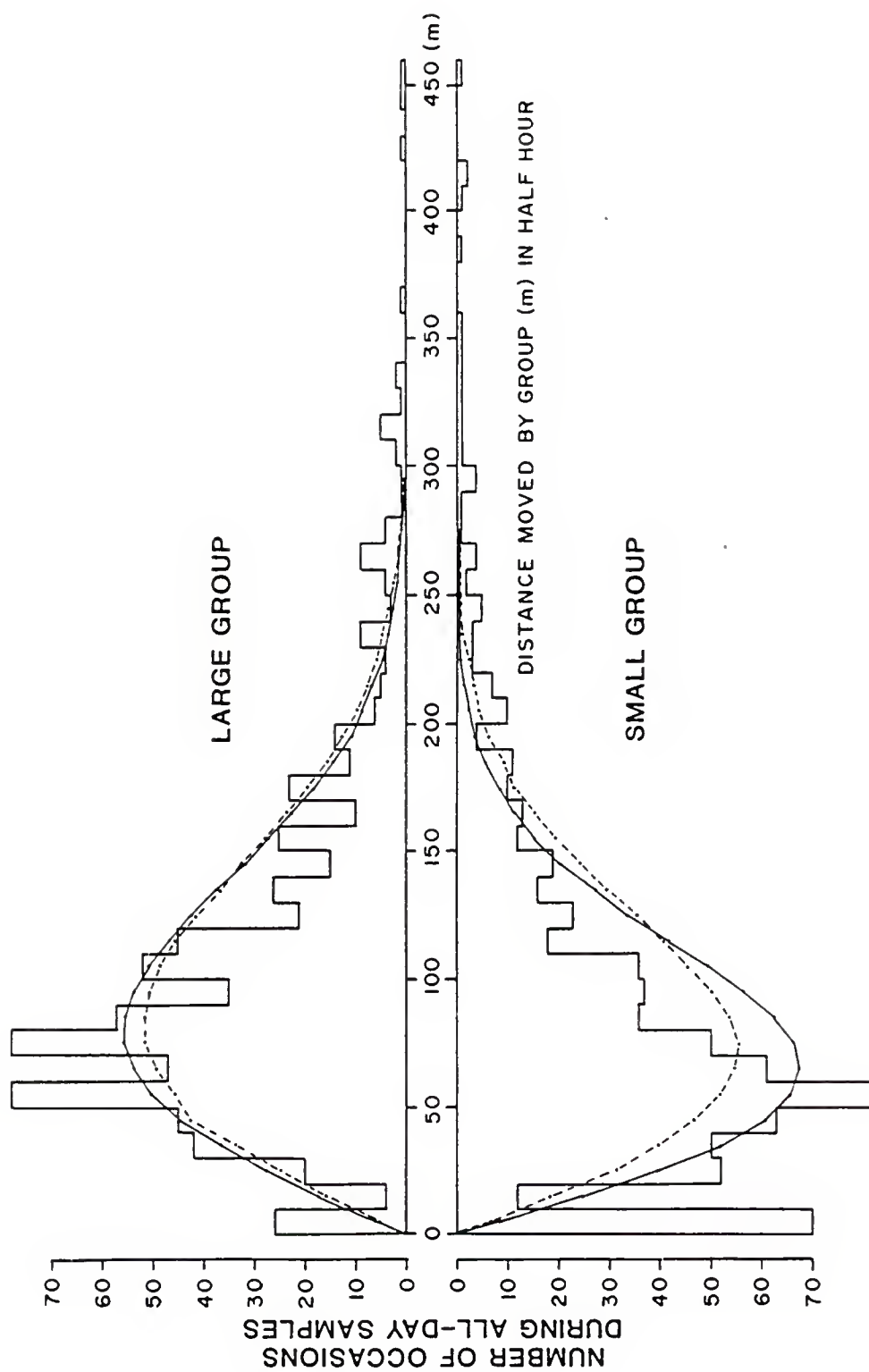
TABLE 3-5

THE HALF-HOUR TURNING ANGLE (DEGREES) IN BOTH GROUPS

Group	Season	Mean	Median	SD	Total records
	Overall	50.9	39.0	44.32	680
LARGE	Wet	48.5	37.0	42.82	269
	Dry	53.4	41.0	45.89	214
	Overall	64.9	53.0	50.17	622
SMALL	Wet	68.3	58.0	51.20	242
	Dry	60.2	46.0	49.85	199

Figure 3-3. Distribution of turning angles between half-hour steps in both groups.
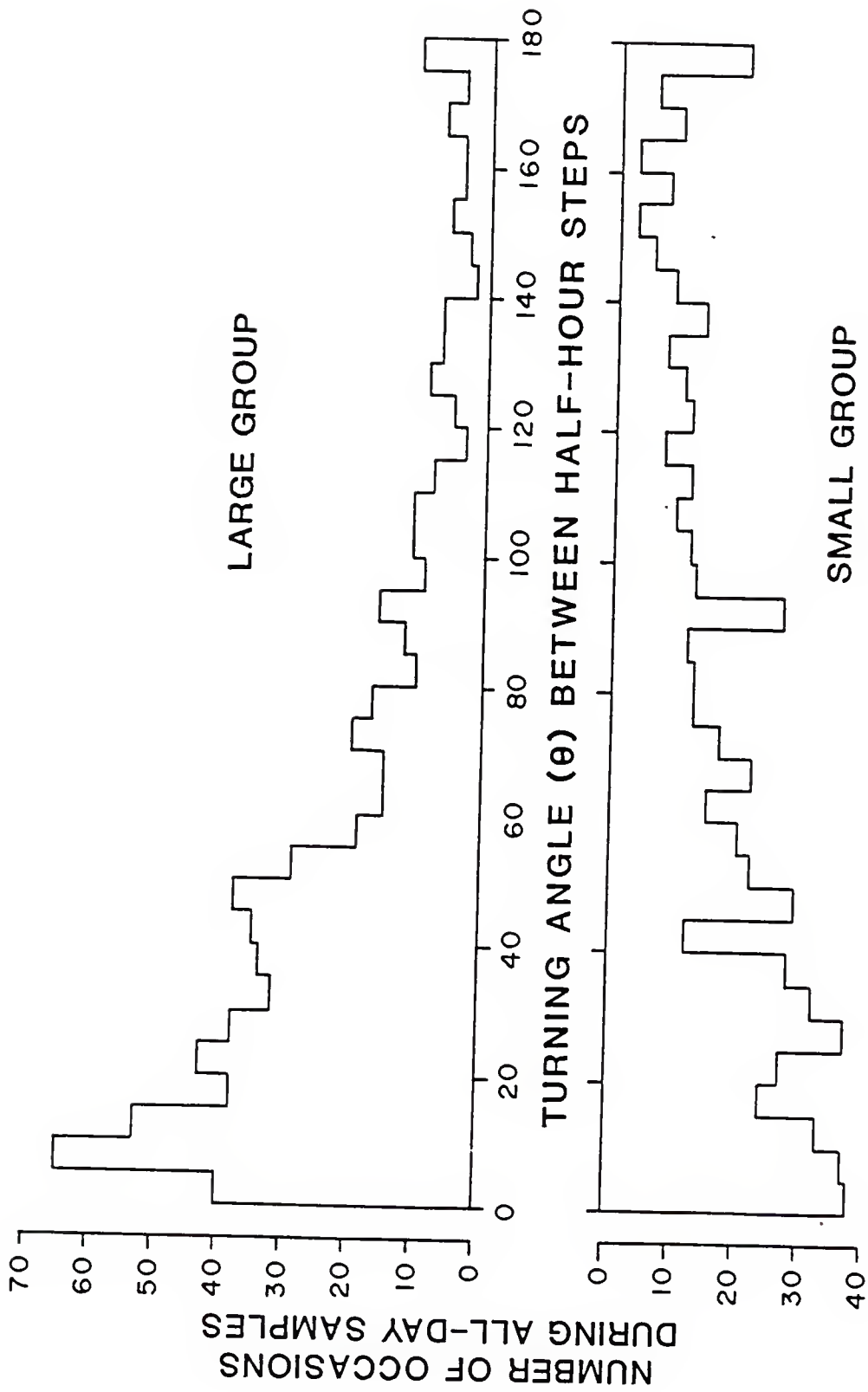
intergroup encounters or animals in smaller groups avoid
intergroup encounters (Chapter V).

Prediction 11: The greater number of animals in larger
groups should result in higher total food requirements. If
larger areas contain larger amounts of food, then larger groups
should use larger areas than smaller groups. I expected that
larger groups would have larger group ranges than smaller groups.

At the end of the study the group range of the LARGE group
had entered 209 one-hectare quadrats while the SMALL group had
entered 174. At comparable lengths of sampling time, the range
of the LARGE group was always larger (Figure 3-4).

Seasonal Comparison

This set of predictions seeks to demonstrate the importance
of intragroup feeding competition by comparing the use of time
and space by animals during periods of resource abundance and
resource scarcity.

Prediction 12: To reduce intragroup feeding competition,
animals in both groups should emigrate more frequently during the
periods of food scarcity (Wrangham, 1980). Robinson (1986)
demonstrated that the dry season is the period of resource
scarcity. Emigrants should be adult females.

However, no instances of adult female emigration from either
group (Table 2-2, 2-3) were recorded.

Figure 3-4. Cumulative area occupied by the study groups, restricted to areas entered during the systematic observations.
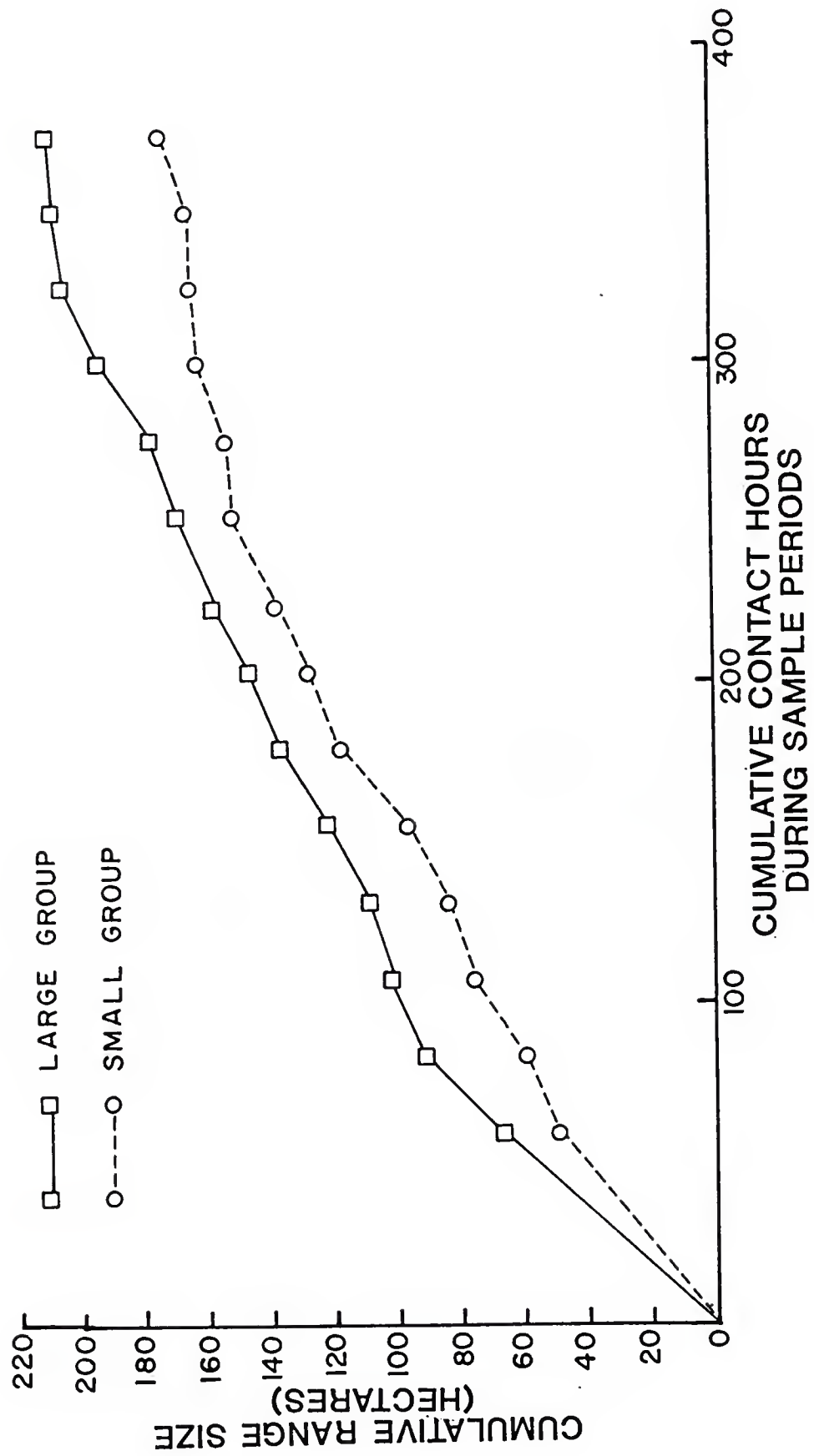
Effect on Use of Resource

Prediction 13: Alternatively, animals in social groups should shift onto "low quality" food during periods of resource scarcity (Wrangham, 1980). Wrangham argued that low quality food is generally homogeneously distributed in the environment and therefore not competed over. I expected that animals in both groups would spend more time foraging for animal material during the dry season. This is because animal material such as insects is more homogeneously distributed than plant material such as fruit (Robinson, 1986).

Both groups spent significantly more time feeding on animal material during the dry than during the wet seasons (Table 3-6; chi-square test, 1df, $p < 0.01$ for both groups).

Effect on Spacing

Prediction 14: Animals may respond spatially to intragroup feeding competition by spreading out through the forest. I expected that nearest-neighbor-distances among animals in social groups would be higher during the period of food scarcity.

Contrary to prediction, the mean nearest-neighbor-distance among animals in both groups was less during the dry season. The mean nearest-neighbor-distances among animals in the LARGE group during the wet and dry seasons were 3.6 m and 3.0 m respectively (Table 3-1). The seasonal difference was statistically significant (Mann-Whitney U-test, n_W =87 instantaneous samples, n_D =92 instantaneous samples, $p < 0.1$). Mean nearest-neighbor-

TABLE 3-6

THE USE OF RESOURCES IN DIFFERENT SEASONS

Resource	LARGE group		SMALL group	
	Wet season	Dry season	Wet season	Dry season
Fruit	33.30	24.30	51.22	50.66
Fruit (excluding figs)	28.11	13.97	34.05	12.63
Plant material	5.38	7.06	4.81	1.82
Animal material	61.32	68.63	43.96	47.51
Total instantaneous samples	1,060	1,374	1,019	823

distances among animals in the SMALL group during the wet and dry
seasons were 3.9 m and 3.5 m respectively. The seasonal
difference was not statistically different (Mann-Whitney U-test,
n_W =134 instantaneous samples, n_D =56 instantaneous samples,
p>0.1).

This failure to verify the prediction may be the result of
animals switching their food during the period of food scarcity
(Prediction 13).

Prediction 15: Animals may spread themselves out more
vertically during the period of food scarcity. I expected that
variation in vertical use of space would be higher among animals
during the dry season.

The coefficients of variation in height were higher in the
dry season than the wet season for both groups. The coefficient
of variation in height for the LARGE group was 85.8% in the dry
season and 59.9% in the wet season. The coefficient of variation
in height for the SMALL group was 49.7% in the dry season and
40.7% in the wet season. The relative variabilities in height
both groups spent in both seasons were significantly different
(Kruskal-Wallis one-way ANOVA, n_W =629 instantaneous samples,
n_D =459 instantaneous samples, p<0.01 in the LARGE group and
n_W =579 instantaneous samples, n_D =304 instantaneous samples,
p<0.01 in the SMALL group).

This same result may be a consequence of animals switching
their food during the dry season (Prediction 13). Low quality
food, by definition, is more dispersed in the environment.

Effect on Time Budget

Prediction 16: If intragroup feeding competition affects
the types of food eaten by animals (Prediction 13), animals in
both groups should spend less time actually feeding but more time
foraging (sensu latu) during the dry season.

Table 3-7 shows how animals in both groups spent their time
in both seasons. Animals in both groups spent more time foraging
(sensu latu) during the dry season. The animals in the LARGE
group spent 22.9% of their time foraging (sensu latu) in the wet
season and 44.3% in the dry season (chi-square test, 1df,
p<0.01). The animals in the SMALL group spent 23.1% of their
time foraging (sensu latu) in the wet season and 51.7% in the dry
season (chi-square test, 1df, p<0.01).

The LARGE group spent less time feeding in the dry season
but the SMALL group spent more time. The animals in the LARGE
group spent 15.0% of their time feeding in the wet season and
12.4% in the dry season (chi-square test, 1df, p<0.1), while
animals in the SMALL group spent 20.6% of their time feeding in
the wet season and 24.3% in the dry season (chi-square test, 1df,
p<0.1).

Prediction 17: The higher intragroup feeding competition
should allow less time for animals in both groups to rest during
the dry season.

The animals in both groups spent less time resting in the
dry season (Table 3-7). The animals in the LARGE group spent
10.6% and 8.7% of their time resting in the wet and dry season

TABLE 3-7

THE TIME BUDGET OF BOTH GROUPS DURING THE WET AND DRY SEASONS

Activity	% Time Large group		% Time Small group	
	Wet season	Dry season	Wet season	Dry season
Forage	22.9	44.3	23.1	51.7
Feed	15.0	12.4	20.6	24.3
Rest	10.6	8.7	14.5	6.6
Move	31.9	25.2	31.7	12.1
Drink	0.7	0.6	0.3	0.4
Socialize	18.1	7.3	6.7	2.6
Non-socialize	0.2	1.5	0.6	2.1
Vigilance	0.6	0.0	2.5	0.2
Total instantaneous samples	3,909	4,070	3,352	2,039

respectively (chi-square test, 1df, p<0.01). The animals in the SMALL group spent 14.5% and 6.6% of their time resting in the wet and dry seasons respectively (chi-square test, 1df, p<0.01).

Prediction 18: To reduce intragroup feeding competition during the dry season, animals should spend more time moving.

Contrary to prediction, animals in both groups spent less time moving in the dry season. The animals in the LARGE group spent 31.9% and 25.2% of their time moving in the wet and dry season respectively (chi-square test, 1df, p<0.01), while the animals in the SMALL group spent 31.7% and 12.1% of their time moving in the wet and dry season respectively (chi-square test, 1df, p<0.01).

Effect on Group Movement and Use of Space

Prediction 19: If a shift to food with more homogeneous distribution is an important mechanism to reduce intragroup feeding competition, groups should move shorter daily distances during the dry season. This follows from Robinson's (1986) demonstration that daily travel distances are lower when animals are foraging on homogeneously distributed resources.

The average half-hour step length was lower in the dry season than in the wet, for the LARGE group but not for the SMALL group. The mean half-hour step length for the LARGE group was 97.4 m and 90.2 m in the wet and dry seasons respectively (Table 3-4), a difference that was statistically significant (Mann-Whitney U-test, n_L =284 records, n_S =234 records, p<0.01). The

mean half-hour step length in the SMALL group was 85.8 m and 71.7
m in the wet and dry seasons respectively. These means are not
significantly different (Mann-Whitney U-test, n_W =284 records,
n_D =227 records, p>0.05).

This suggests that the shift of food is an important
mechanism of reducing intragroup feeding competition especially
during the dry season.

Prediction 20: The shift to homogeneously distributed food
should also affect half-hour turning angles between seasons.
Robinson (1986) reported a weak relation across months between
average turning angle and the proportion of homogeneously-
distributed food in the diet.

The half-hour turning angles in different seasons were not
significantly different in either group. The mean turning angles
in the LARGE group during the wet and dry season were 48.5^o and
53.4^o respectively (Table 3-5; Figure 3-5). Those in the SMALL
group were 68.3^o and 60.2^o in the wet and dry seasons
respectively. Seasonal comparisons of turning angles were not
significantly different in either group (Mann-Whitney U-test,
n_W =269 records, n_D =214 records, P>0.1 in the LARGE group; n_W =242
records, n_D =199 records, p>0.1 in the SMALL group).

Prediction 21: Animals should occupy a smaller area in the
dry season, because they spend more time feeding on food
homogeneously distributed in space.

The SMALL group used a smaller area during the dry season
but the LARGE group used a slightly larger area. The areas

Figure 3-5. Distribution of turning angles between half-hour steps in both groups during wet and dry seasons.

LARGE GROUP
WET SEASON

LARGE GROUP
DRY SEASON

SMALL GROUP
WET SEASON

SMALL GROUP
DRY SEASON

TURNING ANGLES BETWEEN HALF-HOUR STEPS

% RECORDS
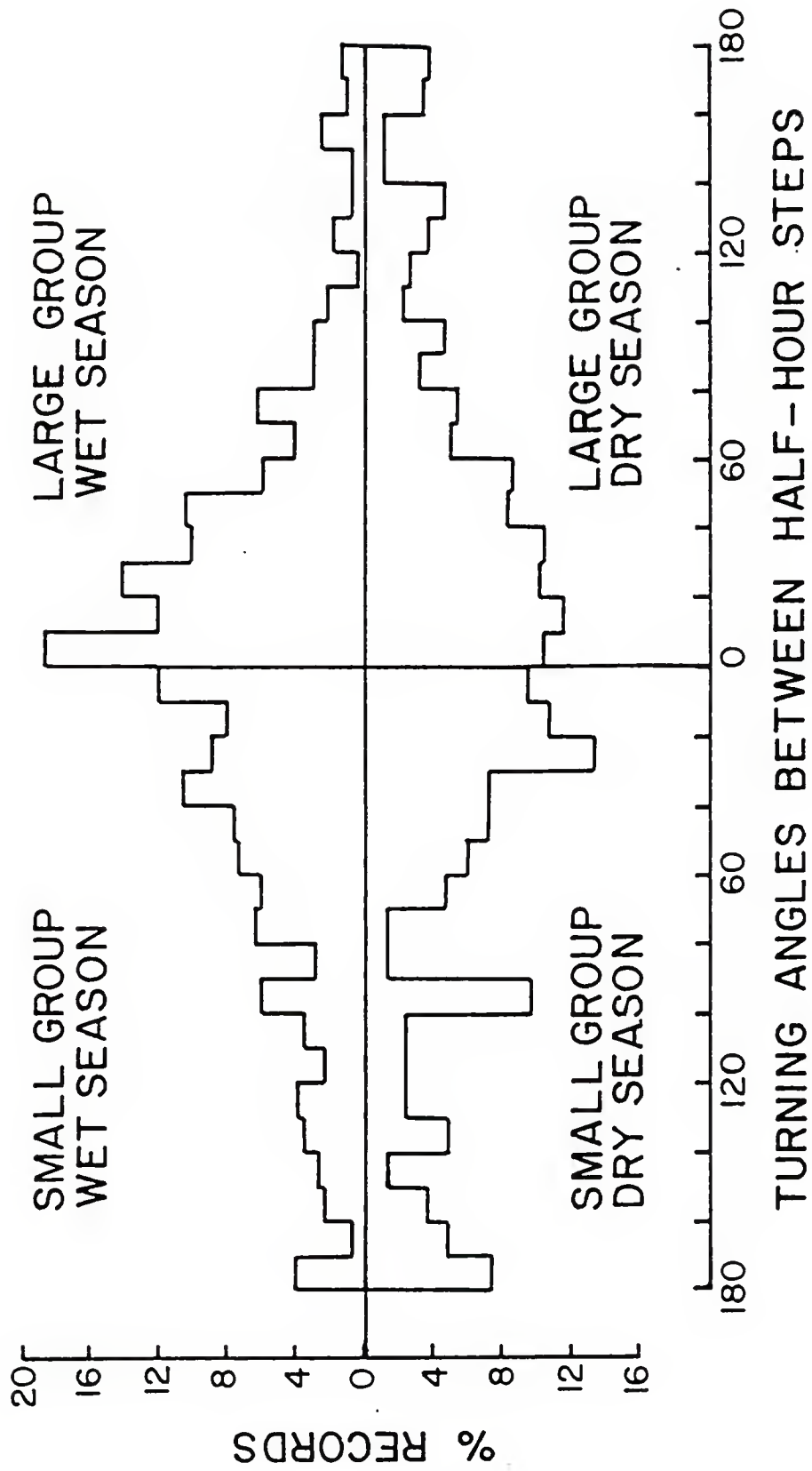
covered by the SMALL group were 87 and 47 ha during a comparable period in the wet and dry seasons respectively. Home range areas in the LARGE group were 98 and 107 ha in the wet and dry seasons respectively.

Discussion

There have been a number of studies showing the importance of intragroup feeding competition on social living. With the increase in group size, animals spend less time feeding (van Schaik et al., 1983a) and more time moving (Green, 1978; van Schaik et al., 1983a). Animals in large groups also stayed away from each other to avoid intragroup feeding competition (Green, 1978). Intragroup feeding competition may also result in longer day-range lengths (Waser, 1977b; Green, 1978; van Schaik et al., 1983a, Dunbar, 1984; Sharman and Dunbar, 1982; de Ruiter, in press), and larger group ranges in larger groups (Iwamoto and Dunbar, 1983; Takasaki, 1981; Stacey, 1986; Suzuki, 1979; Davidge, 1978; Makwana, 1978; van Schaik and van Hooff, 1983). Animals in a group may also switch their food in order to avoid intragroup feeding competition during periods of food scarcity (Oppenheimer, 1968; Hladik, 1975; Dittus, 1977; Robinson, 1986; de Ruiter, in press).

This study suggests that intragroup feeding competition is important in structuring vertical use of space by a group of monkeys. However, variation in vertical use of space may also result from variation in resource abundance at different heights in different seasons. Nevertheless there is still more

agonistic interaction in larger groups and this might structure vertical use of space.

Intragroup feeding competition did not affect invertebrate capture success but did affect fruit feeding.

This study suggests that moving is a behavioral mechanism to reduce intragroup feeding competition. Larger groups move farther and have a greater tendency to move forwards than smaller groups. Large groups also use larger areas.

The effect of group size on the types of food eaten require special attention. The types of food eaten by large groups may be the result of intragroup feeding competition or the priority of access to resources (see Chapter V).

The results in this chapter cannot be used to support or reject Wrangham (1980) or van Schaik (1983)'s hypotheses. Both hypotheses accept the effect of intragroup feeding competition on social living. The differential use of resources by animals in different groups suggests the importance of intergroup feeding competition on social living (Chapter V).

CHAPTER IV
GROUP SIZE AND VULNERABILITY TO PREDATORS

Introduction

Both Wrangham (1980) and van Schaik (1983) recognized a
reduction of vulnerability to predators as an important factor
for group living in primates. Van Schaik (1983) considered
vulnerability to predators as a primary factor while Wrangham
(1980) considered it to be of secondary importance. To prove that
living in groups can reduce vulnerability to predators of animals
in a group will not prove or disprove either Wrangham's or van
Schaik's hypothesis.

The presence of other individuals in a group 1) can reduce
the probability that a given animal will be detected by a
predator (Hamilton, 1971; Treisman, 1975), 2) increase the
probability that predators will be detected by some animals in
the group (Pulliam, 1973; Treisman, 1975; Kenward, 1978), 3)
increase the probability that the animals will deter the attack
of predators (DeVore, 1965; Eisenberg et al., 1972) and that even
if the group is attacked, an individual can avoid being a victim
(Hamilton, 1971; Jarman, 1974).

In forest primates, animals in larger groups may detect
predators from a greater distance or faster than animals in
smaller groups (van Schaik et al., 1983a, 1983b). In an area

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with only terrestrial predators, animals in small groups may
spend more time off the ground (van Schaik et al., 1983b; de
Ruiter, in press).

This chapter will show indirect evidence that by living in
groups, animals reduce their vulnerability to predators. Animals
in large groups spend less time vigilant and more time on the
ground. This evidence, however, is not a conclusive
demonstration that by living in groups animals reduce their
vulnerability to predators.

Methods

Sample Periods

During this study, I completed 16 paired observation
periods. Three pairs were made in the summer of 1982 and the
remainder in 1983-1984. Each pair lasted for two days in each
group, except for two periods in summer 1982 in which five days
of observations were made on each group.

The wet season data were derived from six paired periods
from June to November, 1983. The dry season data were derived
from five paired observation periods from December 1983 to April
1984.

Behavioral Sampling and Use of Time

Each systematic observation day (0600-1800) was divided into
24 half-hour sample periods for the LARGE group and 48 fifteen-

minute periods for the SMALL group. Instantaneous samples of behavior (Altmann, 1974) were made on each individual, five seconds after the animal was first located in each sample period. No individual was sampled more than once in a sample period. Except for defining a "vigilance" category, I adopted the same categories of behavior used by Robinson (1986). This included nine broad categories: foraging, feeding, moving, resting, self cleaning, social grooming, playing, vigilance, other social and non-social behavior. Foraging is defined as looking for and feeding on invertebrate prey. Feeding is defined as actually ingesting food and is virtually restricted to items of plant origin. The foraging category has more subcategories than any others (see details in Robinson, 1986). During foraging I recorded whether an item was ingested during the five seconds immediately following a record, and this allowed me to quantify capture success. Vigilance was defined as the activity when animals were alert and looking around but were not foraging or feeding.

Use of Vertical Space

The height above ground was noted every time a behavioral observation was made. The heights were lumped into 5 categories: ground (=0), 1-5, 6-10, 11-15, and 16-20 m from the ground.

Data Analysis

Statistical analysis relied on SPSSx version 2.1 (SPSS, Inc., 1986). Most analyses used non-parametric statistics (Siegel, 1956) except where indicated. Use of parametric tests followed Sokal and Rohlf (1981). When non-parametric tests were used with a large set of data, a sample was randomly selected from the appropriate data using option 4 in SPSSx (SPSS, Inc., 1986).

Results

Cebus olivaceus monkeys were seen to mob and to give alarm calls in the presence of aerial and terrestrial predators. Potential terrestrial predators included jaguars (Panthera onca), ocelots (Felis pardalis), tayras (Eira barbara), and boas (Boa constrictor). Monkeys also gave alarm calls to caimans (Caiman crocodilus) and collared peccaries (Tayassu tajacu). Monkeys gave alarm calls to the following birds: hook-billed kites (Chondrohierax uncinatus), black vultures (Coragyps atratus), green ibises (Mesembrinibis cayennensis) and rufous-vented chachalacas (Ortalis ruficauda).

Prediction 1: If the animals in large groups have a higher probability of detecting terrestrial predators, then the animals in large groups should spend less time in vigilance. By living in groups, the probability of some animal detecting a predator is higher (Bertram, 1980), and therefore individuals can be less vigilant.

Animals in large groups spend less time in vigilance. Table 3-3 shows the use of time by animals in both groups. Animals in the LARGE group spent less time in vigilance (0.9% versus 1.5%) (chi-square test, 1df, p<0.01).

Prediction 2: The animals in large groups should spend more time on the ground. The high probability of detecting terrestrial predators by animals in large groups should allow them to exploit a foraging microhabitat where they might be more vulnerable to predators.

The animals in the LARGE group spent more time on the ground than the SMALL group (19.2%, n_L =13630 instantaneous samples versus 3.2%, n_S =9419 instantaneous samples; chi-square test, 1df, p<0.01). The average heights off ground of animals in the LARGE and SMALL groups were 7.3 and 9.9 m respectively (Table 4-1). The animals in the LARGE group also spent more time on the ground than the SMALL group throughout the day (Figure 4-1).

An alternative hypothesis that makes the same prediction is that the vertical distribution of space is related, not to the predator vulnerability, but to the use of resources. Animals in both groups spent more time on the ground when they were foraging for invertebrates (Figure 4-2). Animals in large groups foraged more for invertebrates, perhaps because of increased intragroup feeding competition (see chapter III).

Prediction 3: The animals in both groups should spend less time in vigilance during the dry season than the wet season. Because trees are deciduous during the dry season, the visibility

TABLE 4-1

THE HEIGHT ABOVE GROUND (m) SPENT BY BOTH GROUPS

Group	Season	Mean	Median	SD	Total records
	Overall	7.28	5.0	5.078	13630
Large	Wet	9.24	10.0	5.530	3909
	Dry	4.23	5.0	3.631	4070
	Overall	9.89	10.0	4.362	9419
Small	Wet	10.40	10.0	4.254	3352
	Dry	7.32	5.0	3.635	2039

Figure 4-1. Change through the day in the median height off
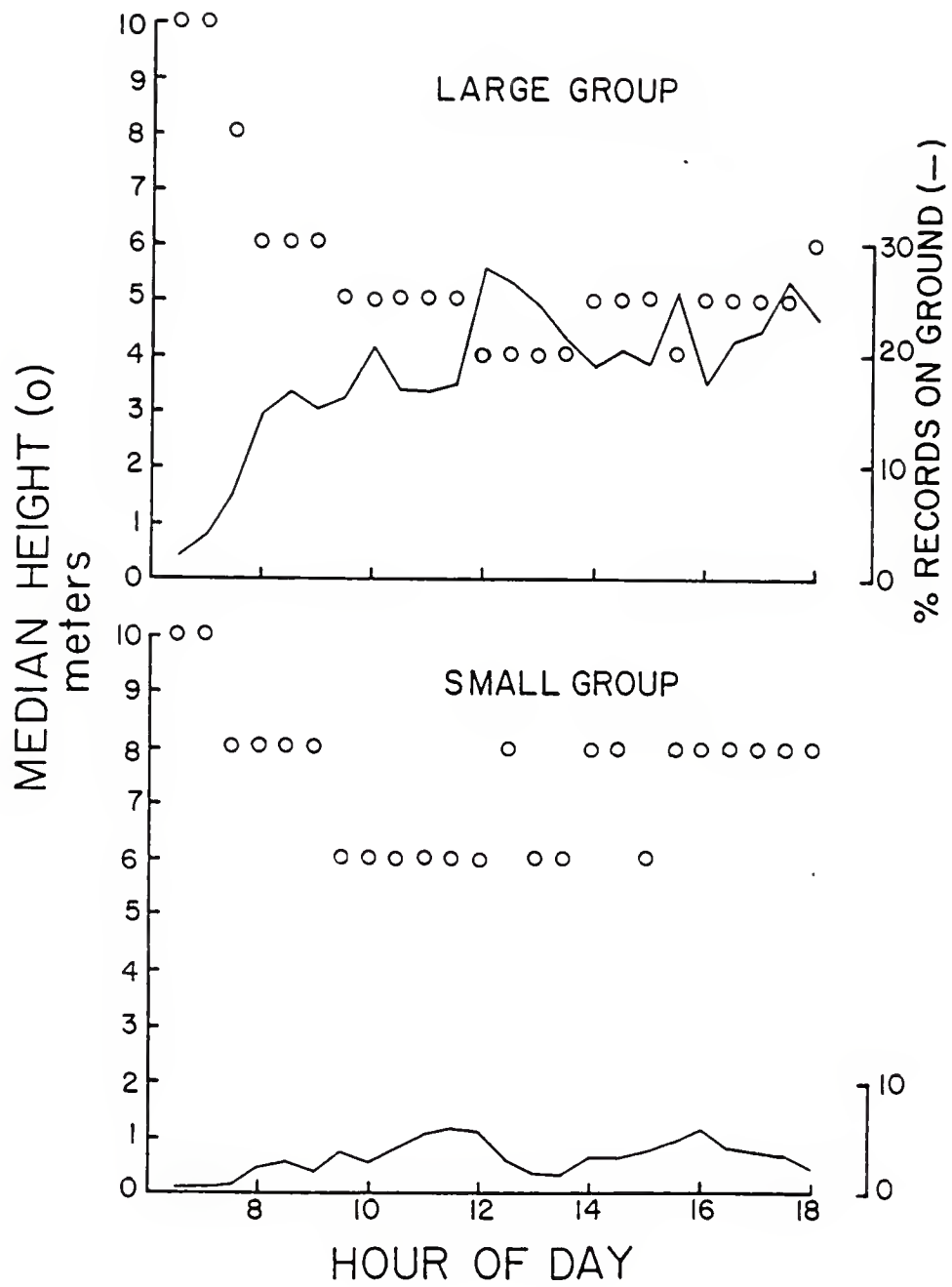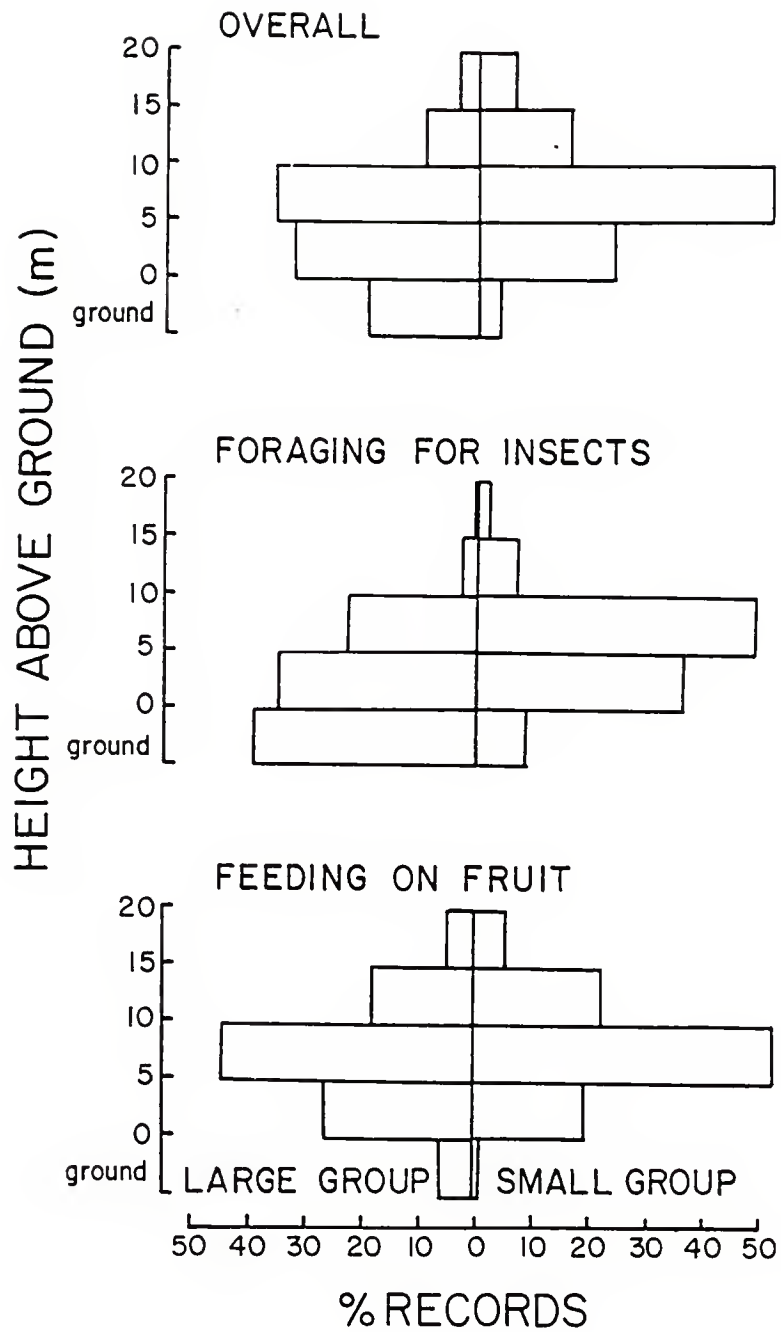ground and % of records on ground in both groups.

Figure 4-2. Histogram showing % of records in relations to
height off ground for overall, during foraging for insects and
feeding on fruit.

during this season is higher, and animals need not be as vigilant.

Animals in both groups spend more time in vigilance during the wet season than during the dry season. The animals in the LARGE group spent 0.6% and 0% of their time in vigilance during the wet and dry season respectively, a significant difference (chi-square test, 1df, p<0.1). The animals in the SMALL group also spent more time in vigilance during the wet season (2.5%) than during the dry season (0.2%) (chi-square test, 1df, p<0.01).

Prediction 4: The animals in both groups should spend more time off the ground in the wet season. I reasoned that it is harder to detect predators during the wet season (Prediction 3) and animals in both groups can reduce vulnerability to predators by spending more time off the ground.

Animals in both groups spent less time on the ground during the wet season. The animals in the LARGE group spent 12.5% and 33.2% on the ground in the wet and dry season respectively, a significant difference (chi-square test, 1df, p<0.01). The animals in the SMALL group spent 1.8% and 8.5% on the ground in the wet and dry seasons respectively, a seasonal difference which was significant (chi-square test, 1df, p<0.01). The animals in both groups spent more time higher in the trees in the wet season than the dry season (Table 4-1).

One alternative explanation is that resources were more common on the ground during the dry season. Another explanation is that the ground was flooded during the wet season, and therefore was less available as a foraging microhabitat.

Discussion

A number of studies have shown indirect benefits from social living by reducing vulnerability to predators. By living in social groups, animals may detect predators at a greater distance (van Schaik et al., 1983b), spend less time in vigilance (van Schaik et al., 1983b; de Ruiter, in press), and spend more time on the ground (van Schaik et al., 1983a; de Ruiter, in press). There is no study of primates showing the direct effect of group size on vulnerability to predators. A study on birds, however, showed no effect of group living on vulnerability to predators (Page and Whitacre, 1975, p. 82, reanalysing by using group size of one and more than one: chi-square test, 1df, $p > .0.1$).

In this study area, the only potential aerial predator that has been reported to take Cebus olivaceus is the Harpy Eagle, Harpia harpyja (Rettig, 1978), but this species has not been observed at the study site. The smaller Ornate Hawk-Eagle, Spizaetus ornatus, however, is present. Terrestrial predators include jaguars (Panthera onca) and ocelots (Felis pardalis) but most are primarily active during the night (Schaller and Crawshaw, 1980; Ludlow, 1986). Boas (Boa constrictor) may be able to take the monkeys (Chapman, 1986).

This study showed that animals in large groups spent less time in vigilance. But this does not mean that animals in large groups are less vulnerable to predators. It is debatable that the degree of arboreality is solely a product of vulnerability to predators. It may be the result of intragroup feeding competition.

The results reported in this chapter cannot be used for supporting or rejecting either hypothesis. This study does not show any conclusive correlation between group size and vulnerability to predators.

CHAPTER V
GROUP SIZE AND INTERGROUP FEEDING COMPETITION

Introduction

Intergroup feeding competition has been recognized by
Wrangham (1980) as a main selective pressure for living in a
social group. Larger groups should be able to displace smaller
groups. Van Schaik (1983), on the other hand, downplayed the
importance of intergroup feeding competition in selecting for
social living. A demonstration that animals in large groups have
feeding advantages because of the size of their group will
support Wrangham's hypothesis.

Good examples for intergroup feeding competition in animals
can be seen in animals that defend space. In primates, these
species usually emit loud vocalizations that maintain spacing.
Examples include gibbons (Hylobates lar, Carpenter, 1940), titi
monkeys (Callicebus moloch, Mason, 1968), howler monkeys
(Alouatta palliata, Carpenter, 1934), Hanuman langur (Presbytis
entellus, Jay, 1965), white-cheeked mangabey (Cercocebus
albigena, Waser, 1975, 1977a), and black and white colobus
monkeys (Colobus guereza, Marler, 1969). Of the other species
that do not defend exclusive areas, some demonstrate an
intergroup hierachy and a group rank. Group rank is determined

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by group size in rhesus monkeys (<u>Macaca</u> <u>mulatta</u>, Southwick et al., 1965), but not in <u>C.</u> <u>albigena</u> (Waser, 1977a).

This chapter will show that there is intergroup feeding competition in capuchin monkeys, <u>Cebus</u> <u>olivaceus</u>, and that animals in large groups have a greater access to resources. Large groups dominate smaller groups and intergroup encounters affect animals' use of time, group movement, use of space and access to resources.

Methods

Group Sizes and Censusing

The identity and sizes of groups were obtained from regular censuses. Whenever I encountered other groups, I followed them for as long as possible. Some of the groups were totally unhabituated while others had been censused regularly since 1977. I noted all distinctive individual characteristics of group members and gave names to any newly recognized individuals. A final group count was arrived at only after repeated censuses. I noted the locations of followed groups every half-hour. Establishing group identities was essential to the study of intergroup relations.

Intergroup Relations

Intergroup encounters were noted both during the systematic observation periods and opportunistically when I was following

other groups. An intergroup encounter is defined behaviorally
as one in which animals from at least two groups were in visual
contact. The time and location of each intergroup encounter was
noted. Such opportunistic sampling is unbiased with respect to
the outcome and identity of the group interaction. However, data
on the relative frequency of interactions involving the LARGE and
SMALL groups depended only on counts taken during systematic
observation periods.

Sample Periods

During this study, I completed 16 paired observation
periods. Three pairs were made in the summer of 1982 and the
remainder in 1983-1984. Each pair lasted for two days in each
group, except for two periods in summer 1982 in which five days
of observations were made on each group. Observations on use of
space were from the 14 paired sample periods.

To quantify the effect of intergroup encounters on use of
time, I compared time budgets on days with intergroup encounters
and days without encounters in both wet and dry seasons. Wet
season months were from June to November, 1983, while dry season
months were from December 1983 to April 1984. Three and two
observation periods were obtained for the LARGE group during the
wet and dry seasons respectively, while two and three periods were
obtained for the SMALL group during the wet and dry seasons
respectively.

Behavioral Sampling and Use of Time

Each systematic observation day (0600-1800) was divided into
24 half-hour sample periods for the LARGE group and 48 fifteen-
minute periods for the SMALL group. Instantaneous samples of
behavior (Altmann, 1974) were made on each individual, five
seconds after the animal was first located in each sample period.
No individual was sampled more than once in a sample period.
Except for defining a "vigilance" category, I adopted the same
categories of behavior used by Robinson (1986). This included
nine broad categories: foraging, feeding, moving, resting, self
cleaning, social grooming, playing, vigilance, and other social
and non-social behavior. Foraging is defined as looking for and
feeding on invertebrate prey. Feeding is defined as actually
ingesting food and is virtually restricted to items of plant
origin. The foraging category has more subcategories than any
others (see details in Robinson, 1986). During foraging I
recorded whether an item was ingested during the five seconds
immediately following a record, and this allowed me to quantify
capture success. Vigilance was defined as the activity when
animals were alert and looking around but were not foraging or
feeding.

All social interactions were also noted opportunistically
using the ad libitum method (Altmann, 1974). In other words, I
recorded all social interactions whenever they were noted.

Movement and Use of Space

Before I began my study, an extensive trail system was established by Robinson, Fragaszy and de Ruiter. The trails were marked with colored plastic flags and marked aluminum tags every 25 meters. The trail system was approximately 60 km long. During my study period, I maintained this system and also extended trails into areas that were used by the SMALL group, mainly in the northern part of the study site (Figure 3-1).

Locations of the study groups were noted every half-hour starting at 0600 h until 1800 h on all systematic observation days. The center of mass of the group was carefully placed on the map. The center of mass is defined as the approximated location of a center of a group. When intergroup encounters occurred I noted down time and location of encounters.

To study group movements, two variables were measured from the observed group paths. These were half-hour movements and half-hour turning angles. Half-hour movements measure the distances from two centers of mass in consecutive half-hour periods. Half-hour turning angles measure angular deviations from straight ahead between consecutive half-hour movements. Both half-hour movement and turning angle have been used before in primate studies (Waser, 1976; Robinson, 1986).

To study the use of space of the two groups, one-hectare quadrats were used. The quadrat locations and sizes are identical to those of Robinson (1986). Each half-hour location of the center of mass was considered as a single score when the use of area of the two groups was calculated. Home range was

calculated by the total number of quadrats occupied during the half-hour locations in a specified period of time.

As the time and location of intergroup encounters were also noted, I was able to analyse the effects of intergroup encounters on group movement. The locations of intergroup encounters were also assigned in the same quadrat system as above.

To correlate the use of space with the distribution of food, data on the distribution of fruit trees from the study by Dr. Robinson and new data obtained at the end of my study were used. The numbers of trees of different species were counted along the existing North-South trails (Robinson, 1986). The transect lines were then divided into sample quadrats. Each sample quadrat was 100 m in length and 2.5 m in width on either side of the trail (Robinson, 1986). This 500 sqm quadrat running North-South through the center of each 1 ha quadrat was taken as representative of that quadrat. We successfully covered 125 of 209 quadrats or 59.8 % in the LARGE group's range and 88 of 174 quadrats or 50.6 % in the SMALL group's range.

To examine more closely the group overlap in range, I spent as much time as possible following all the possible groups in the study area during May 23 to June 29, 1984. This overlapped with the annual census period of Dr. Robinson, which allowed me to match the identity of the groups with Robinson (1986). This period was at the end of my study period so that most groups were habituated. Information on the location of other groups was also obtained from Dr. Robinson. When I followed other groups, I noted the location every half-hour.

To study the vertical use of space of the group, the height above ground was noted every time a behavioral observation was made. The heights were lumped into 5 categories: ground (=0), 1-5, 6-10, 11-15, and 16-20 m from the ground.

Every time a behavioral observation was made, the distance and identity of nearest neighbors was noted whenever possible. The distance was estimated in 1 m intervals up to 10 m.

Use of Resources

During behavioral observations, I noted the object types in which animals were foraging. When the monkeys fed, the food was classified as to animal or plant origin.

Plant material used by the animals was identified by various methods. Most of the important plant species used by the animals were shown to me by Dr. Robinson at the beginning of my study. Some plants were identified and tagged. I also consulted the local people or resident botanists at the ranch. Three references which I used for plant identification were Ramia (1974), Hoyos (1979) and Steyermark and Huber (1978). Most plants used by the monkeys were identified to species. In contrast, food of animal origin was rarely identified.

Morisita's index was used as a measure of the consistency or patchiness in space of a particular tree species in the forest (Robinson, 1986; Poole, 1974). Morisita's index for each species of trees was obtained from Robinson (1986).

Sucrose density of fruits was measured with a Bausch and Lomb sucrose refractometer (see also Janson, 1985; White and Stiles, 1985).

Data Analysis

Statistical analysis relied on SPSSx version 2.1 (SPSS, Inc., 1986). Most analyses used non-parametric statistics (Siegel, 1956) except where indicated. Use of parametric tests followed Sokal and Rohlf (1981). When non-parametric tests were used with a large set of data, a sample was randomly selected from the appropriate data using option 4 in SPSSx (SPSS, Inc., 1986).

To compare variation such as in half-hour movements, coefficients of variation were compared. The logarithm to the base 10 was also taken for each datum to estimate relative variability (Lewontin, 1966). This allowed me to use Kruskal-Wallis one-way ANOVA to test the significant differences (Sokal and Braumann, 1980).

Results

Intergroup Relations

Intergroup encounters occurred on 51.6 % and 67.7 % of the systematic observation days in the LARGE and SMALL groups respectively ($n_L = n_S = 31$ days). The behavior of group members during intergroup encounters has been described by Robinson

(1986). Intergroup encounters occurred during all times of the day but mostly frequently in the morning (Figure 5-1). The probability of an intergroup encounter was higher during the wet season in both groups ((LARGE group: 75% of days in the wet season (n_W =12 days) versus 20% of days during the dry season (n_D =10 days); SMALL group: 83.3% of days in the wet season (n_W =12 days) versus 50% of days during the dry season (n_D =10 days)).

Intergroup encounters occurred 20 times in the LARGE group but 44 times in the SMALL group, during a comparable sample of 31 observation days.

PREDICTION 1: If intergroup feeding competition has contributed significantly to the evolution of primate sociality, then larger groups must spatially displace smaller groups. If the outcome of intergroup encounters between pairs of groups is predictable, then this can be used to define the relative rank of groups.

Between 1977 and 1982 the SMALL group displaced other groups only once during 12 intergroup encounters (8.3%; Robinson, 1986, Table 16). During my study period it won three of 65 encounters (4.7%; Table 5-1). The only group that the SMALL group displaced was the BROWN group, another small group of 10 animals. Of the five encounters, BROWN displaced SMALL twice (40%) indicating that the ability of these groups to displace one another was unclear.

Between 1977 and 1982 the LARGE group displaced other groups on 49 of 60 intergroup encounters (81.7%) (Robinson 1986, Table

Figure 5-1. Change through the day in the frequency of intergroup encounters.
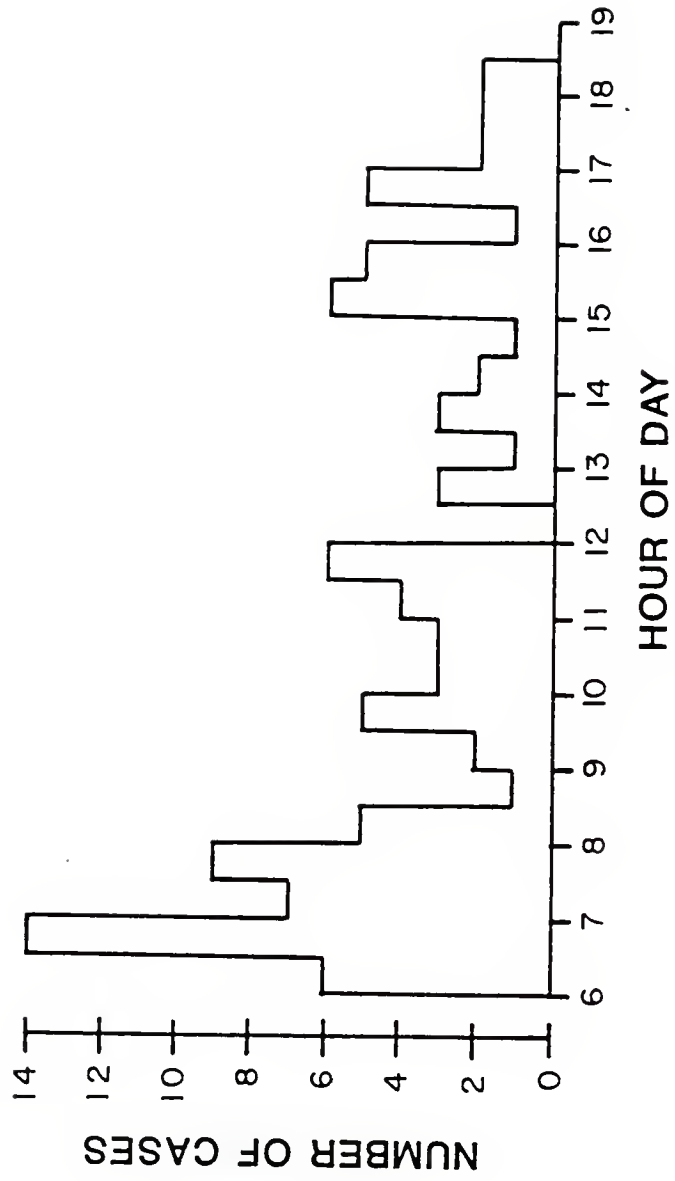
TABLE 5-1

WINNERS AND LOSERS OF INTERGROUP ENCOUNTER DURING MY STUDY PERIOD

Winner \ Loser	Cinn	Nort	Larg	Red	Oro	Oran	Grey	Blue	Pale	Pink	Brow	New	Smal	Unkn
Cinn	X								2					
Nort		X	4										1	
Larg			X	4		2					7		8	9
Red				X	X								2	
Oro					X	X							1	
Oran						X	X						3	2
Grey							X	X					1	
Blue								X	X					
Pale									X	X				
Pink										X	X		1	
Brow											X	X	2	
New												X	7	
Smal													X	
Unkn			1								3		25	X
Group Size	+40	+40	36	28	+25	22	19	15	14	14	10	9	5	
% Win	100	100	86	73	100	71	100	100	0	100	17	100	5	
Number of encountered groups	1	2	+4	+2	1	+3	2	1	1	1	4	1	+10	
Total encounters	2	5	35	15	2	7	4	1	2	1	12	7	64	

16). During my study period the LARGE group won 30 of 35 encounters (85.7%) (Table 5-1). The LARGE group consistently lost to the GREAT NORTHERN and CINNAMON groups, two very large groups of more than 40 members. On occasion, it also lost to the CHESTNUT and ORANGE groups. The ORANGE group was equal in size to LARGE group, the CHESTNUT group was smaller.

The number of different groups that SMALL group encountered was greater than the number encountered by LARGE group: 10 different groups versus 4. This suggests that SMALL group was pushed into interstitial areas occupied at least occasionally by a large number of other groups.

During the eight year period from 1977 to 1984, the LARGE group always displaced the SMALL group.

Use of Time

Prediction 2: If intergroup encounters are a form of intergroup feeding competition, then intergroup encounters will affect the use of time of animals in small groups. I expected that on days when intergroup encounters occurred, smaller groups would spend more time moving and foraging for invertebrates than larger groups. Smaller groups should also rest less, and feed less on fruit. Intergroup encounters should have little or no effect on time budgets in larger groups.

Intergroup encounters negatively affect the use of time in some activities in the SMALL but not in the LARGE group. Table 5-2 compares allocation of time to different activities by animals in both the LARGE and SMALL groups, during both the wet and dry

TABLE 5-2

THE EFFECT OF INTERGROUP ENCOUNTER ON TIME BUDGETS (%)
OF ANIMALS IN BOTH GROUPS DURING THE WET AND DRY SEASONS

| Activity	% Time LARGE group				% Time SMALL group			
	Wet season		Dry season		Wet season		Dry season	
	Intergroup encounter				Intergroup encounter			
	Yes	No	Yes	No	Yes	No	Yes	No
Forage	33.1	30.7	38.8	52.2	27.5	22.5	45.9	53.1
Feed	16.9	16.0	15.8	11.5	25.0	25.6	24.3	24.4
Rest	8.5	8.0	8.4	5.4	10.7	14.0	8.4	8.9
Move	28.9	31.8	26.7	22.7	31.2	26.5	15.3	10.0
Drink	0.1	0.1	0.6	0.7	0.5	0.2	0.2	0.3
Socialize	11.5	13.2	8.8	6.2	4.0	9.1	3.3	1.7
Non-socialize	0.3	0.2	0.8	1.3	0.2	1.1	2.4	1.3
Vigilance	0.7	0.0	0.1	0.0	0.9	1.0	0.2	0.3
Total instantaneous samples	952	924	855	753	552	614	633	631
Number of days	3	3	2	2	2	2	2	2

seasons. Animals in the SMALL group spent more time moving and foraging (sensu latu) on encounter days during the dry and wet seasons respectively (chi-square test, 1df, p<0.01). But intergroup encounters did not affect % time animals in the SMALL group spent feeding and resting in either season, moving in the wet season, and foraging (sensu latu) in the dry season (chi-square test, 1df, p>0.01). Intergroup encounters did not negatively affect % time animals in the LARGE group spent on moving, foraging (sensu latu), feeding and resting in either season (chi-square test, 1df, p>0.01).

Group Movement

Prediction 3: Intergroup encounters should affect the pattern of group movement. This effect should be greater in smaller groups. I expected that day-ranges and half-hour movements would be longer on days with intergroup encounters, especially in small groups. The direction of movement of small groups should also be altered by intergroup encounters.

The length of the day-range correlated with the number of intergroup encounters in the SMALL group (r_s =0.63, n=26 days, p<0.01; Figure 5-2). Ranges were longer on days on which intergroup encounters occured. There was no such correlation in the LARGE group (r_s =0.14, n=29 days, p>0.1). Average half-hour movements were longer on days that included intergroup encounters in the SMALL group (Mann-Whitney U-test, n=234 records, n=492

Figure 5-2. The regression lines of the length of day ranges and the number of intergroup encounters per day in both groups.
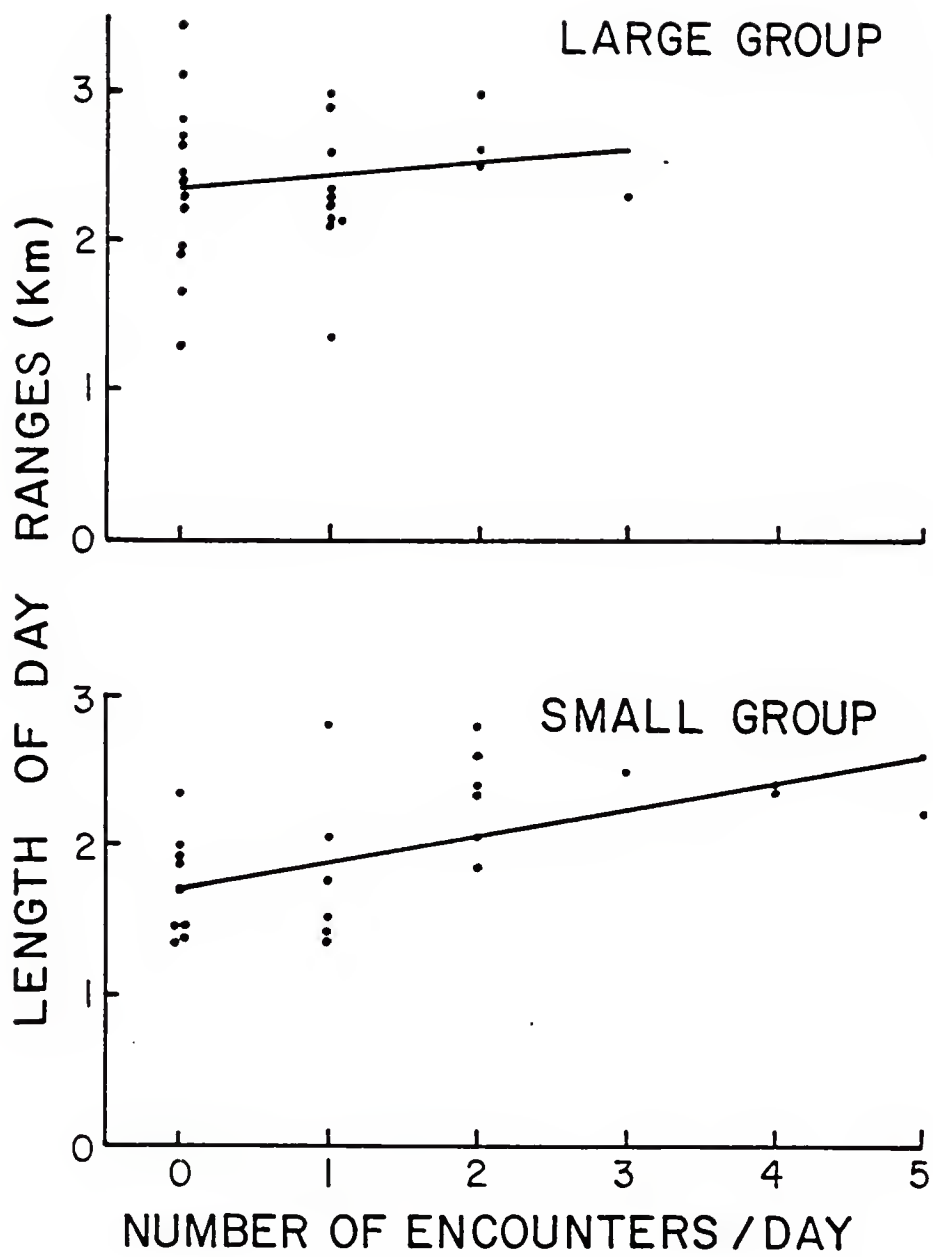
records, p<0.05) but not in the LARGE group (Mann-Whitney U-test, n=355 records, n=379 records, p>0.1).

Intergroup encounters also influenced the direction of group movements in the SMALL group more than the LARGE group. The half-hour turning angles immediately following an intergroup encounter were larger in the SMALL group. The mean half-hour turning angle following encounters in the SMALL group was 87.8^{o} (with median=86.5^{o}, SD=57.74^{o}, n=35 records) while in the LARGE group, it was 54.3^{o} (with median=39.0^{o}, SD=49.40^{o}, n=14 records). These angles were significantly larger than mean angles of turning outside the context of intergroup interactions only in the SMALL group (Mann-Whitney U-test, n_{L}=14 records, n_{S}=35 records, p<0.01; Figure 5-3).

Use of Space

Groups in the study area have highly overlapping home ranges (Robinson, 1986, Figure 23). Figure 5-4 shows that areas used by the two main study groups were also used by at least eight other groups during a month's sample in 1986. During the study period an index of overlap (Holmes and Pitelka, 1968) between the LARGE and SMALL groups is 0.4099.

Prediction 4: Animals in smaller groups should restrict themselves to areas away from clumped food resources. The foraging pattern of the non-tufted capuchin monkeys (Terborgh, 1985; Robinson, 1986) has been described as extended movements between clumped food resources. If they are denied access to

Figure 5-3. Distribution of turning angles between half-hour steps after intergroup encounters in both groups.
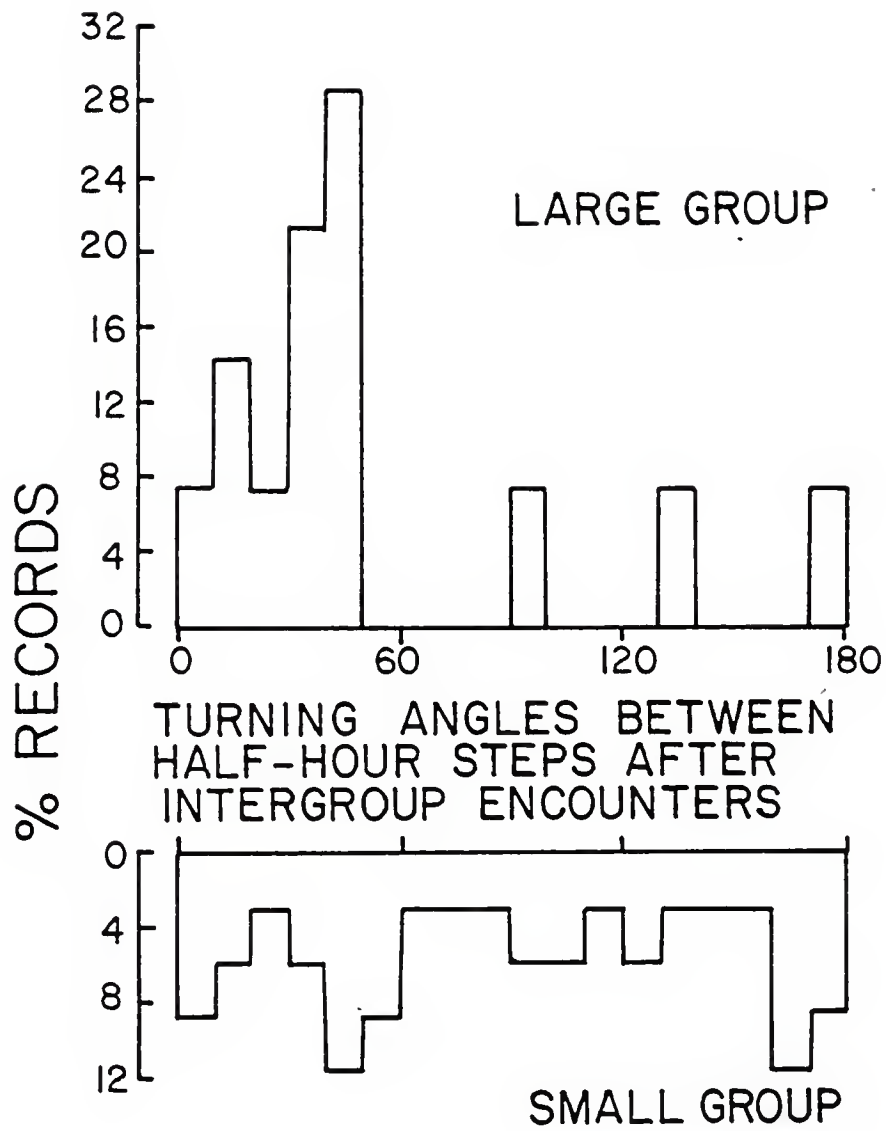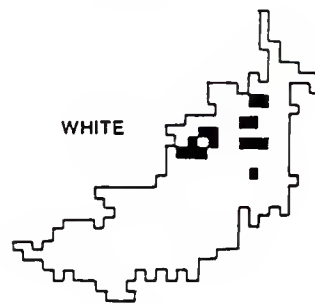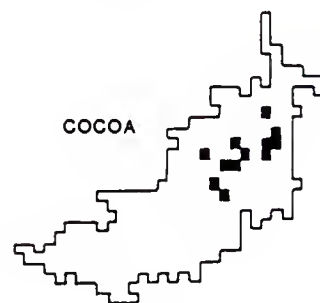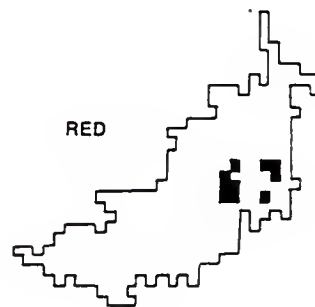
LARGE GROUP

% RECORDS

TURNING ANGLES BETWEEN
HALF-HOUR STEPS AFTER
INTERGROUP ENCOUNTERS

SMALL GROUP

Figure 5-4. Locations of ten groups of monkeys in relation
to combined ranges of the LARGE and SMALL group (265 ha) during
May 23 and June 29, 1984.
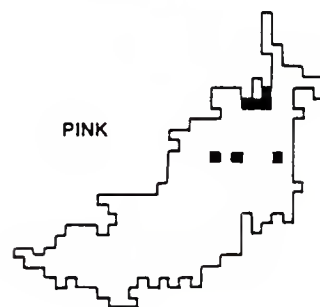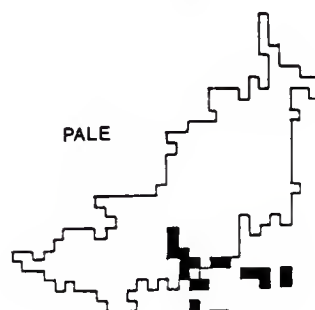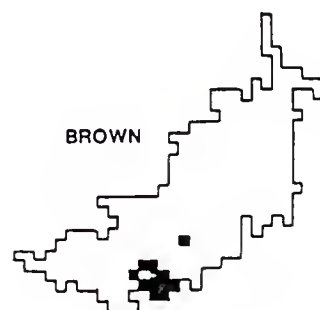
clumped resources, animals in smaller groups will not range over
a large area but instead concentrate their activities in a few
specific areas. I expected that quadrats of intergroup
encounters would be more localized (at specific clumped
resources) in the range of large groups, and small groups would
concentrate their activities in certain areas.

Locations of intergroup encounters were more localized in
the range of the LARGE group (Figure 5-5). Figures 5-6 and 5-7
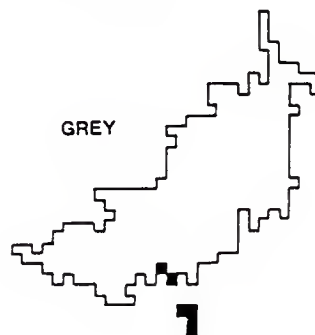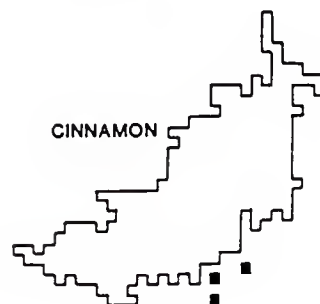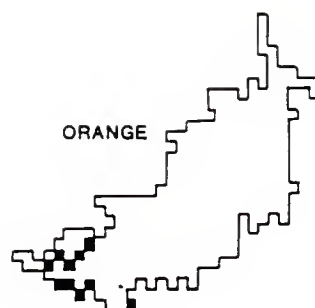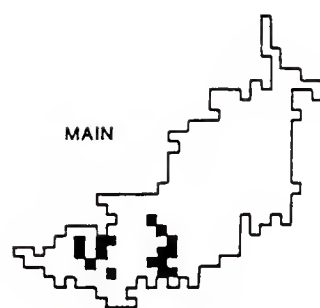show how both groups used their ranges. The LARGE group spread
its time more evenly over its range than did the SMALL group.
The quadrats of heavy use were also clumped in certain areas of
the SMALL group's range. The use of space of the LARGE group was
more homogeneous. There are more quadrats with higher frequency
of use in the SMALL group (Figure 5-8). The LARGE group occupied
8.1, 21.1 and 40.7 per cent of its home range in 25, 50 and 75
per cent of its time respectively (Figure 5-9). The SMALL group
occupied 5.2, 17.8 and 39.1 per cent of its range in 25, 50 and
75 per cent of its time respectively (Figure 5-9).

Prediction 5: If animals in different groups avoid one
another or if groups displace one another from certain areas, the
use of space by different groups should be negatively correlated.
I expected that the use of area of overlapping by large and small
groups would be negatively correlated.

In the area of overlap, there was no negative correlation
between the quadrat occupancies of the LARGE and SMALL groups
(r_s =0.0407, n=118 quadrats, p>0.1). Both groups used these
areas of mutual overlap as heavily (Wilcoxon-pairs signed-ranks

Figure 5-5.   Locations of intergroup encounters in both groups.

LARGE GROUP
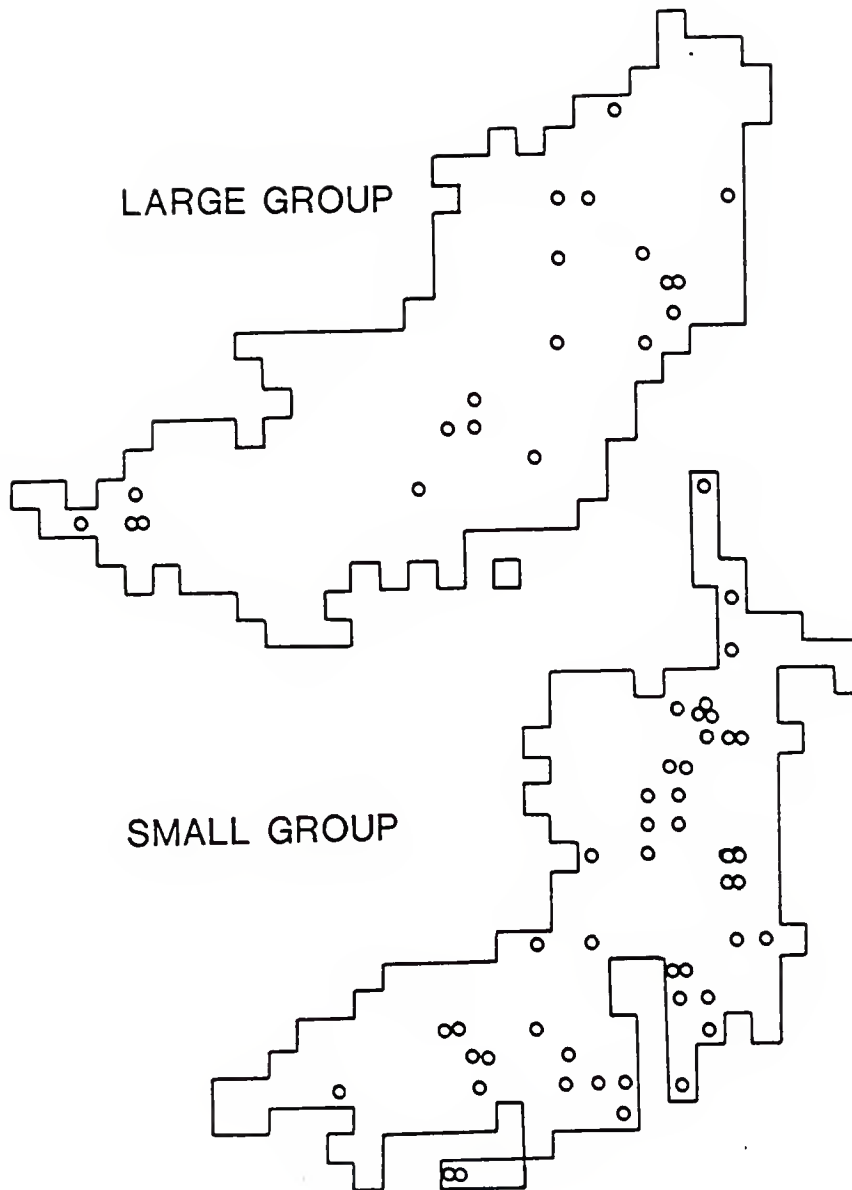
SMALL GROUP

Figure 5-6. Quadrat occupation by the LARGE group.

LARGE GROUP

PERCENT USE

☐ 0.01-0.49

▨ 0.50-1.49

▨ 1.50-2.49
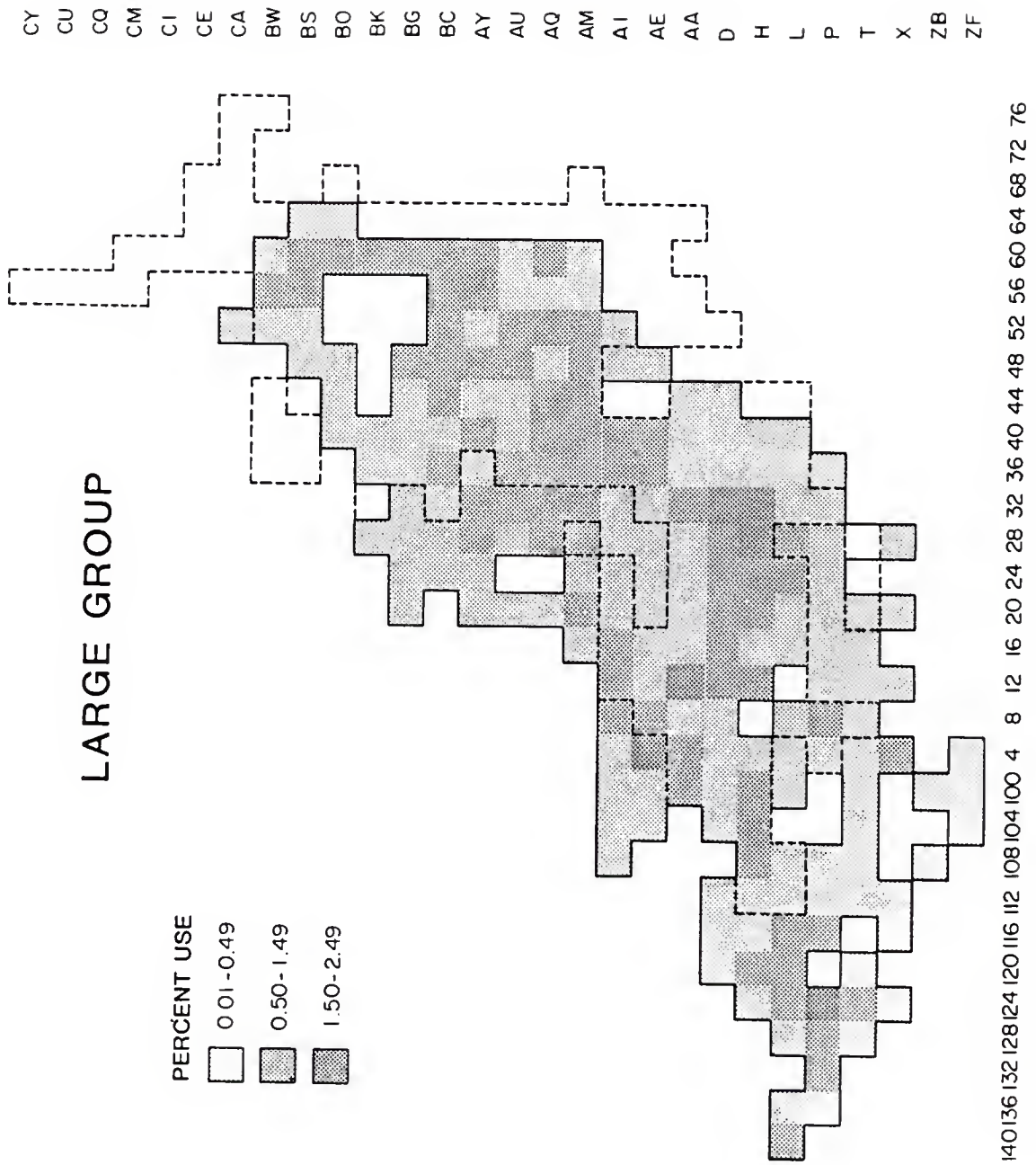
Figure 5-7. Quadrat occupation by the SMALL group.

SMALL GROUP

PERCENT USE

0.01-0.49

0.50-1.49

1.50-2.49

2.50-3.49

6.00-6.49

CY
CU
CQ
CM
.CI
CE
CA
BW
BS
BO
BK
BG
BC
AY
AU
AQ
AM
AI
AE
AA
D
H
L
P
T
X
ZB
ZF

140 136 132 128 124 120 116 112 108 104 100 4 8 12 16 20 24 28 32 36 40 44 48 52 56 60 64 68 72 76

Figure 5-8. Frequency distribution of quadrat intensity of use in both groups.

Figure 5-9. Distribution of quadrat occupancy in the LARGE (L) and SMALL (S) groups. Figure plots cumulative hours of occupancy against a ranked order of quadrats. Bar graph illustrates the proportion of the total home range occupied 25%, 50% and 75% of the time.

test, n=118 quadrats, p>0.1). This pattern may have resulted from the use of the area by the other 12 groups during the study.

Use of Resources

Cebus olivaceus monkeys feed on both plant and animal resources. Table 5-3, 5-4, 5-5 and 5-6 show the 30 most important plant items taken by both groups, and the 20 most important object types used by animals while foraging.

The animals in the LARGE group fed more on animal material than did the animals in the SMALL group. Animals in the LARGE group allocated 36.2% and 62.9% of their time to foraging on plant and an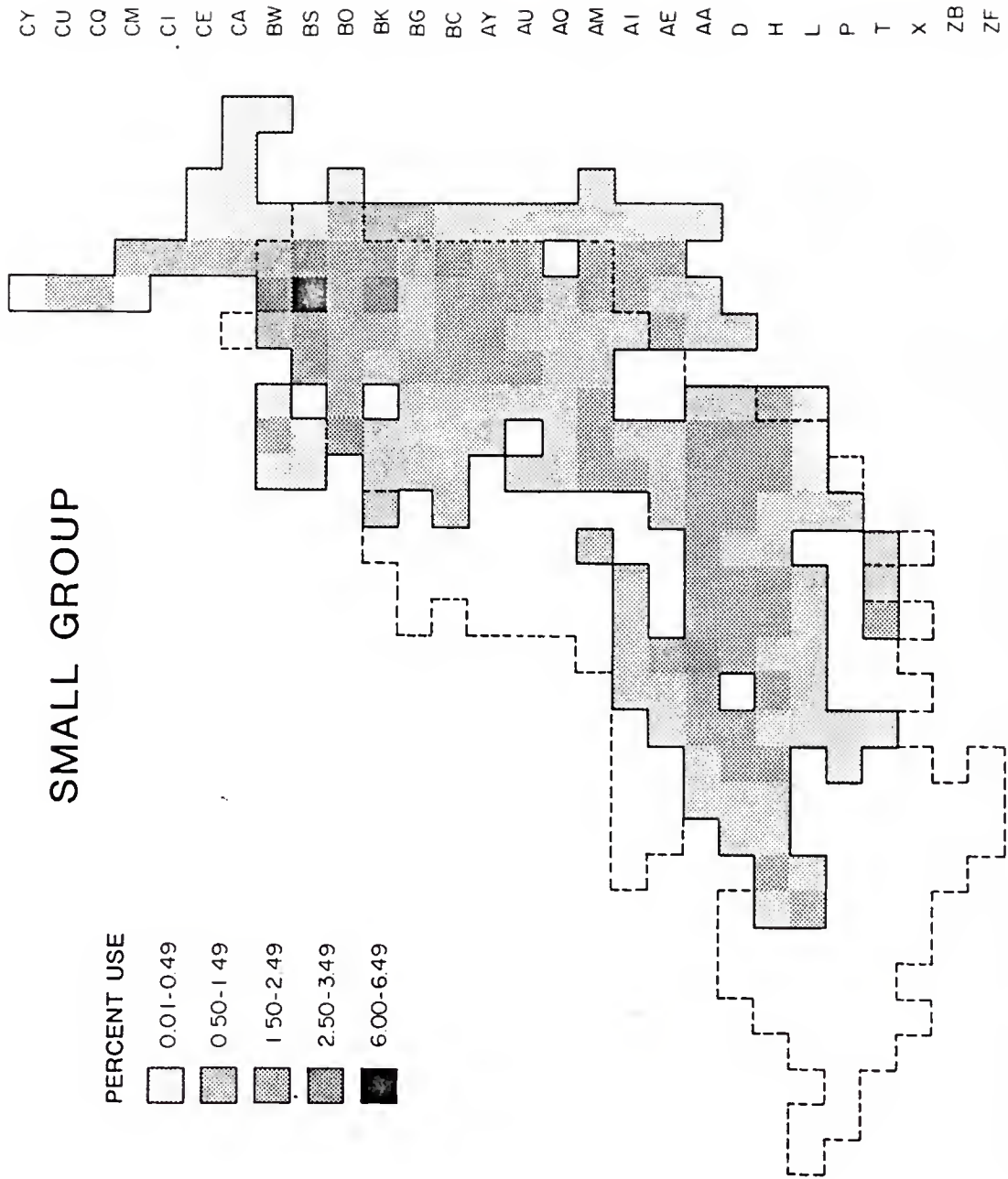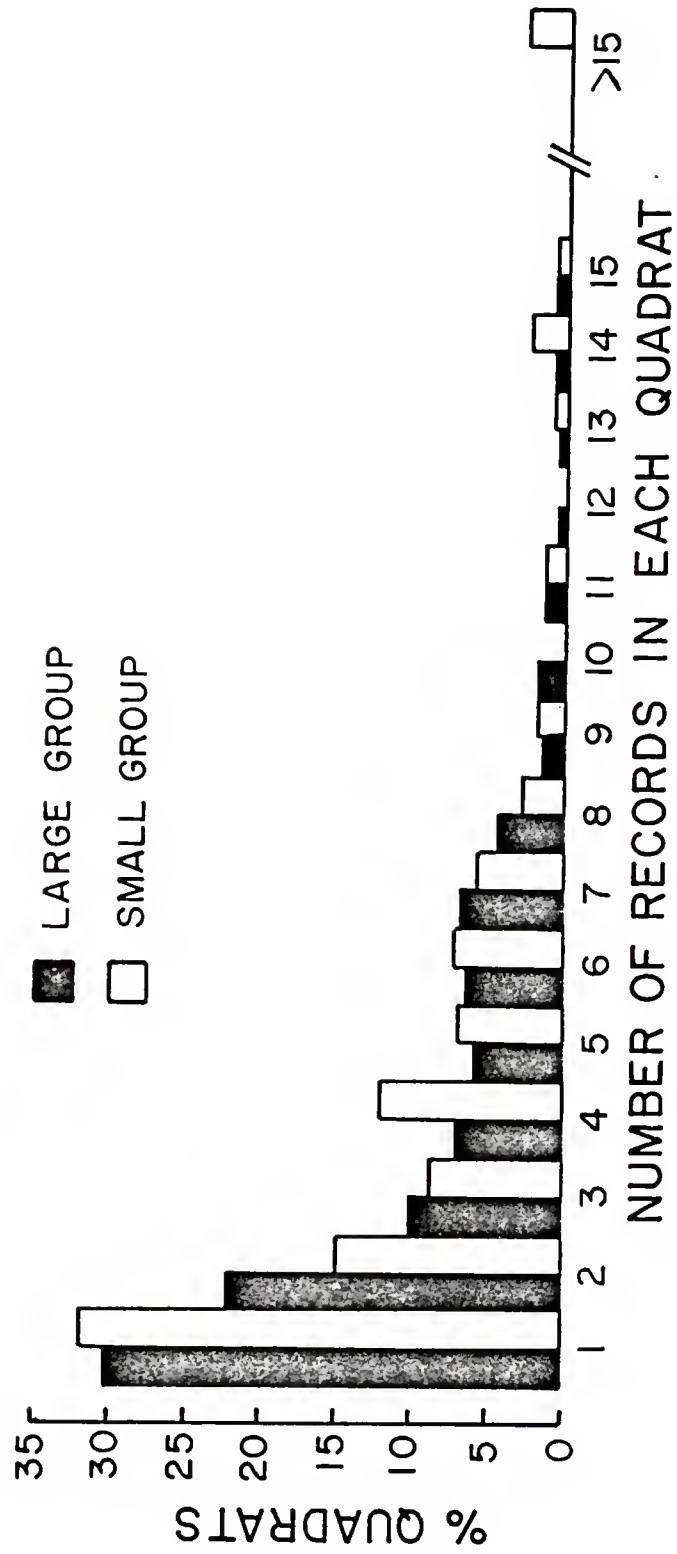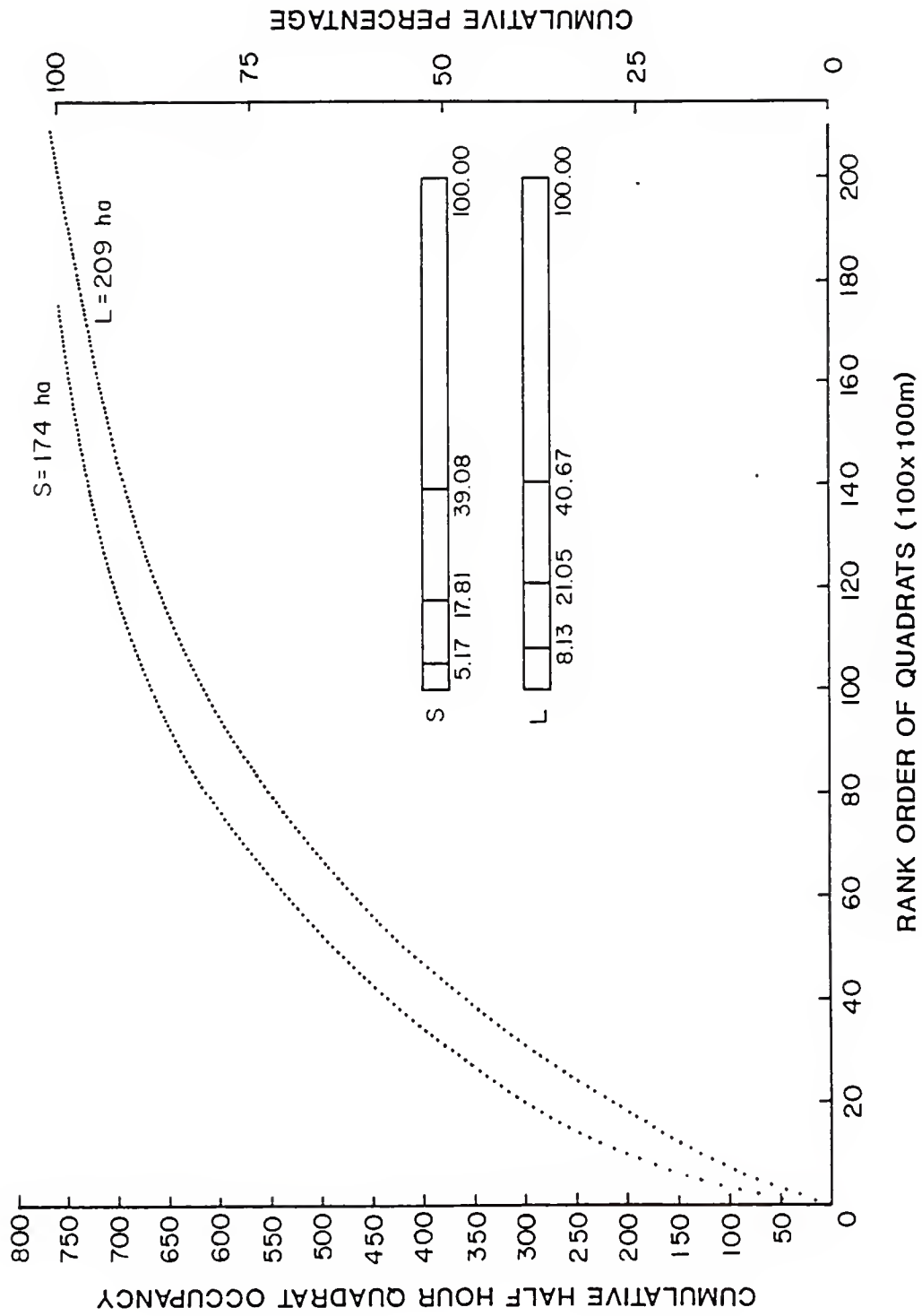imal material respectively. Animals in the SMALL group allocated 50.0% and 47.5% of their time to feeding on plant material and foraging on animal material respectively. Paired comparisons of the 16 observation periods indicated that the LARGE group foraged more for animal material and less for plant material (Wilcoxon matched-pairs signed-ranks test, p<0.01, n=16 pairs, for both animal and plant material). The animals in the SMALL group fed more on figs, Ficus pertusa, than did the animals in the LARGE group (Sign test, p<0.1, n=16 pairs).

Prediction 6: If larger groups have greater priority of access to resources than smaller groups, larger groups should be able to use resources that are patchily distributed in space and relatively uncommon. I expected that animals in larger groups would spend more time feeding on fruit trees with higher values on the Morisita's index.

TABLE 5-3

MOST IMPORTANT PLANT ITEMS IN THE DIET OF ANIMALS
IN THE LARGE GROUP

Rank	Species	Part eaten	Number of records	%
1	Ficus pertusa	Fruit	209	14.3
2	Vitex compressa	Fruit	158	10.8
3	Copernicia tectorum	Palm pith	145	9.9
4	Vitex orinocensis	Fruit	139	9.5
5	Ficus trigonata	Fruit	117	8.0
6	Guazuma tomentosa	Fruit	72	4.9
7	Copaifera officinalis	Fruit	71	4.9
8	Hecatostemon completus	Fruit	68	4.7
9	Copernicia tectorum	Fruit	67	4.6
10	Psychotria anceps	Fruit	63	4.3
11	Zanthoxylum culantrillo	Seed	52	3.6
12	Thalia geniculata	Seed	47	3.2
13	Genipa americana	Fruit	29	2.0
14	Oncidium spp.	Stem	21	1.4
15	Scleria setuloso-ciliata	Seed	19	1.3
16	Randia herbecarpa	Fruit	19	1.3
17	Annona jahnii	Fruit	18	1.2
18	Melothria trilobata	Fruit	10	0.7
19	Cordia collococca	Fruit	9	0.6
20	Spondias mombin	Fruit	7	0.5
21	Hipi hipi	Seed	6	0.4
21	Connarus venezuelanus	Fruit	6	0.4
21	Copernicia tectorum	Cabbage	6	0.4
21	Coccoloba caracasana	Fruit	6	0.4
25	Diospyros ierensis	Fruit	5	0.3
26	Marsdenia undulata	Unripe fruit	4	0.3
27	Bromelia spp.	Fruit	3	0.2
27	Margaritaria scandens	Fruit	3	0.2
27	Melothria trilobata	Unripe fruit	3	0.2
27	Lecythis ollaria	Seed	3	0.2

Totals 1457

TABLE 5-4

MOST IMPORTANT PLANT ITEMS IN THE DIET OF ANIMALS
IN THE SMALL GROUP

Rank	Species	Part eaten	Number of records	%
1	Ficus pertusa	Fruit	311	20.2
2	Guazuma tomentosa	Fruit	154	10.0
3	Vitex compressa	Fruit	145	9.4
4	Copaifera officinalis	Fruit	104	6.8
5	Hecatostemon completus	Fruit	101	6.6
6	Ficus trigonata	Fruit	86	5.6
7	Annona jahnii	Fruit	81	5.3
8	Randia herbecarpa	Fruit	79	5.1
9	Copernicia tectorum	Fruit	60	3.9
10	Psychotria anceps	Fruit	58	3.8
11	Zanthoxylum culantrillo	Fruit	42	2.7
12	Vitex orinocensis	Fruit	35	2.3
13	Combretum fruticosum	Nectar	33	2.1
14	Genipa americana	Fruit	28	1.8
15	Melothria trilobata	Fruit	20	1.3
16	Sterculia apetata	Fruit	16	1.0
17	Cissus sicyoides	Fruit	16	1.0
18	Diospyros ierensis	Fruit	14	0.9
19	Spondias mombin	Fruit	13	0.8
20	Cordia collococca	Fruit	12	0.8
21	Sterculia apetata	Unripe fruit	10	0.7
22	Connarus venezuelanus	Fruit	9	0.6
23	Centrosema pubescens	Flower	6	0.4
23	Orchid	Stem	6	0.4
25	Legume	Young leaf	5	0.3
25	Copernicia tectorum	Unripe fruit	5	0.3
25	Thalia geniculata	Seed	5	0.3
25	Vitex capitata	Fruit	5	0.3
25	Copernicia tectorum	Cabbage	5	0.3
25	Copernicia tectorum	Pith	5	0.3

Totals 1537

TABLE 5-5

THE FIRST 20 OBJECT TYPES IN WHICH THE LARGE GROUP
LOOKED FOR ANIMAL MATERIALS

Rank	Category	Number of records	%
1	Palm nut(1)	335	13.2
2	Ground(2)	234	9.2
3	Leaf litter	207	8.2
4	Dry twig	204	8.0
5	Small snails	193	7.6
6	Caterpillars	177	7.0
7	Dry branches	112	4.4
8	Palm leaves	98	3.9
9	Palm boots	82	3.2
10	Palm rachis	77	3.0
11	Leaves	62	2.4
12	Dry palm leaves	60	2.4
13	Scale insect	55	2.2
14	Bark	46	1.8
15	Twig	41	1.6
16	Branch	39	1.5
17	Dry bough	33	1.3
18	Palm top	32	1.3
19	Dry leaves	23	0.9
20	Big snails	21	0.8
	Totals	2538	

(1) The grubs in the palm nuts are Cocotrypes dactyliperda
Fabricus (identified by Dr. Woodruff).
(2) Foraging for snails (Pomacea spp) and palm nuts.

TABLE 5-6

THE FIRST 20 OBJECT TYPES IN WHICH THE SMALL GROUP
LOOKED FOR ANIMAL MATERIALS

Rank	Category	Number of records	%
1	Dry twigs	231	15.8
2	Dry branches	121	8.3
3	Leaves	119	8.2
4	Caterpillars	117	8.0
5	Barks	69	4.7
6	Palm leaves	53	3.6
7	Palm nuts (1)	52	3.6
8	Twigs	48	3.3
9	Dry palm leaves	43	2.9
10	Samaras (2)	35	2.4
11	Palm boots	32	2.2
12	Leaf litters	32	2.2
13	_Hyla crepitans_	27	1.9
14	Palm top	25	1.7
15	Dry bough	25	1.7
16	Palm rachis	25	1.7
17	Branches	24	1.6
18	Small snails	18	1.2
19	Bough	16	1.1
20	Millipedes	15	1.0
	Totals	1459	

(1) The grubs in the palm nuts are _Cocotrypes dactyliperda_
    Fabricus (identified by Dr. Woodruff).
(2) The young samaras of _Pterocarpus acalapulcensis_ Rose.

Large groups have greater access to fruit trees that are clumped and are relatively uncommon. Table 5-7 shows the rank of fruit species fed on by both groups. For both groups, figs, Ficus pertusa, were the highest ranking fruit. The second most frequently taken fruit by the SMALL group was Guazuma tomentosa, which is widely distributed in space and common (Morisita's index=1.33). Animals in both groups fed heavily on Vitex compressa which, although it is spatially heterogeneous, is relatively common. The third most important fruit on an annual basis for animals in the LARGE group is Vitex orinocensis. Animals in the SMALL group are denied access to this species because trees are uncommon and occur in only a few locations (Table 5-7, see Robinson, 1986).

Prediction 7: The greater access to resources by animals in larger groups should allow these animals to use higher quality fruit than animals in small groups. I expected that animals in larger groups should feed more on fruit high in sugar concentration.

Animals in large groups feed more on fruit high in sugar concentration. During the summer of 1982, the most important fruit source for animals in the LARGE group was Vitex orinocensis, while for animals in the SMALL group, it was Vitex compressa (Table 5-8). Fruits of V. orinocensis contain a higher concentration of sugar than fruits of V. compressa (Table 5-8).

Prediction 8: Because they are denied access to resources animals in smaller groups should not be able to track the spatial

TABLE 5-7

THE TEN MOST IMPORTANT FRUIT FED ON BY BOTH GROUPS IN COMPARISON WITH CLUMPING INDEX (MORISTITA'S INDEX) AND ABUNDANCE RANK

Species	LARGE group % time fed	Rank	SMALL group % time fed	Rank	Morisita's index	Rank	Abundance rank
Ficus pertusa	15.6	1	20.8	1	1.75	8	7
Vitex compressa	11.8	2	9.6	3	4.33	3	9
Vitex orinocensis	10.4	3	2.3	12	9.79	1	11
Ficus trigonata	8.8	4	5.7	6	2.75	6	10
Guazuma tomentosa	5.4	5	10.2	2	1.33	11	4
Copaifera officinalis	5.3	6	6.9	4	3.24	5	12
Hecastostemon completus	5.1	7	6.7	5	1.67	9	6
Copernicia tectorum	5.0	8	4.3	9	1.51	10	3
Psychotria anceps	4.7	9	3.9	10	2.07	7	2
Zanthoxylum culantrillo	4.0	10	2.8	11	1.33	11	5
Annona jahnii	2.1	13	5.4	7	3.63	4	8
Randia hebecarpa	1.4	15	5.3	8	4.47	2	1

Note: Morisita's index and abundance of each fruit tree were from Robinson (1986)

TABLE 5-8

FOUR TYPES OF FRUIT FED ON BY BOTH GROUPS DURING SUMMER 1982,
IN RELATION TO SUGAR CONCENTRATION

| Rank | Species | % fed by | | Sugar concentration (g solute per 100 g solution, ^{o}Brix) |
		LARGE group	SMALL group	
1	Vitex orinocensis	35.43	7.77	19.0
2	Annona jahnii	5.03	12.78	14.0
3	Ficus pertusa	27.14	21.80	13.0
4	Vitex compressa	15.83	23.81	12.5

Note: All % time feeding on each kind of fruit are significantly
       different at the level of 0.01 (Z-test).

distribution of fruit trees. I expected that the correlation between the use of area and the distribution of fruit trees would be higher in larger groups than in smaller groups.

Table 5-9 shows the Spearman rank correlation of the LARGE group's use of space with the spatial distribution of fruit trees. Correlations are positive for eight of the 10 most important tree species, and significant for two of them. Use of space is also positively correlated with the five most important species of fruit trees.

Table 5-10 shows the Spearman rank correlation of the SMALL group's use of space and the spatial distribution of fruit trees. Correlations are not significant for the 10 most important tree species, however for six of the species there was a negative trend.

Discussion

Intergroup encounters may affect group movement (Struhsaker, 1974). The type and magnitude of this effect may differ from one group to another. This is because groups of animals in a study area may be ranked according to the outcome of intergroup encounters (Deag, 1973; Robinson, 1986). Larger groups usually have the ability to displace smaller groups (Southwick et al., 1965; Vessey, 1968; Lindburg, 1971; Struhsaker, 1967; but see Hausfater, 1972; Struhsaker, 1980; Anderson, 1981; Mehlman, 1984). It has been shown that in blue monkeys after group fission, the small group occupied a less favored area (Cords and Rowell, 1986).

TABLE 5-9

CORRELATION BETWEEN QUADRAT OCCUPATION BY THE LARGE GROUP AND
THE SPATIAL DISTRIBUTION OF THE TEN MOST IMPORTANT FRUIT TREES

Rank	Species	r_s	p	Total trees
1	Ficus pertusa	.0790	.191(ns)	151
2	Vitex compressa	.2045	.011(*)	112
3	Vitex orinocensis	-.2123	.009(**)	57
4	Ficus trigonata	.0176	.423(ns)	70
5	Guazuma tomentosa	.0785	.192(ns)	551
6	Copaifera officinalis	-.1828	.021(*)	8
7	Hecatostemon completus	.1205	.090(ns)	257
8	Copernicia tectorum	.1176	.096(ns)	971
9	Psychotria anceps	.2426	.003(**)	325
10	Zanthoxylum culantrillo	.0601	.253(ns)	424
	1 and 2 ranking species combined	.2376	.004(**)	263
	1,2 and 3 ranking speicies combined	.1217	.088(ns)	316
	1,2,3 and 4 ranking species combined	.0972	.140(ns)	386
	1,2,3,4 and 5 ranking species combined	.1603	.037(*)	934

(1) The test is Spearman rank correlation.
(2) The data are available for 125 of the 209 quadrats (59.81 %)
    making up the range.
(3) * and ** is a statistically significant difference at the
    0.05 and 0.01 level respectively.

TABLE 5-10

CORRELATION BETWEEN QUADRAT OCCUPATION BY THE SMALL GROUP AND
THE SPATIAL DISTRIBUTION OF THE TEN MOST IMPORTANT FRUIT TREES

Rank	Species	r_s	p	Total trees
1	Ficus pertusa	-.1544	.075(ns)	84
2	Guazuma tomentosa	-.1536	.077(ns)	356
3	Vitex compressa	.1083	.158(ns)	108
4	Copaifera officinalis	.0760	.241(ns)	8
5	Hecatostemon completus	-.0568	.300(ns)	159
6	Ficus trigonata	-.1711	.055(ns)	44
7	Annona jahnii	.0214	.422(ns)	63
8	Randia herbecarpa	.1585	.070(ns)	252
9	Copernicia tectorum	-.0253	.407(ns)	579
10	Psychotria anceps	-.0570	.299(ns)	236
1 and 2 ranking species combined		.1899	.038(*)	440
1,2 and 3 ranking species combined		-.0681	.264(ns)	548
1,2,3 and 4 ranking species combined		-.0668	.268(ns)	556
1,2,3,4 and 5 ranking species combined		-.0418	.349(ns)	715

(1) The test is Spearman rank correlation.
(2) The data are available for 88 of the 174 quadrats (50.57 %)
    making up the range.
(3) * and ** is a statistically significant difference at the
    0.05 and 0.01 level respectively.

This study showed that <u>Cebus</u> <u>olivaceus</u> groups can be ranked according to the outcome of intergroup encounters. Large groups tend to displace smaller groups. Intergroup encounters affect both the lengths of day-range and directions of group movement of smaller groups but not larger groups. Small groups move greater distances, their movement directions are changed, and their use of space is restricted to certain areas. As a consequence, larger groups have higher priority of access to clumped and restricted resources than smaller groups.

These results supported Wrangham's hypothesis that by living in social groups, animals derive a feeding advantage through intergroup competition.

CHAPTER VI
CONCLUSION

This study showed that animals in larger groups increased
their feeding efficiencies by being able to displace smaller
groups over clumped and restricted food sources. It also showed
that animals in larger groups coped with higher intragroup
feeding competition. It is difficult to demonstrate, however,
that feeding advantages obtaining from dominating other groups
are higher than the costs due to reduced feeding efficiency as
the result of intragroup feeding competition.

Janson (1985), however, showed that there was higher
intragroup than intergroup feeding competition in Cebus apella by
comparing energy intake of the least and most dominant
individuals within a group and the least and most aggressively
successful groups. Stacey (1986) also demonstrated a
relationship between group size and foraging efficiency in Papio
cynocephalus. Both studies assumed that animals maximize their
mean rate of net energy gain (see also Pyke et al., 1977).
However, some studies have suggested that animals might be
sensitive to both the variance and mean of energy intake (e.g.
Oster and Wilson, 1978; Thompson et al., 1974; Caraco, 1980;
Real, 1980; Stephens, 1981).

This study showed that subordinate groups or smaller groups
were interrupted more during feeding than larger groups. Smaller

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groups encountered other groups more often and moved backwards after intergroup encounters. Smaller groups also sometimes avoided intergroup encounters. Both reasons resulted in the smaller groups feeding less on clumped and restricted food resources than larger groups.

This study has not demonstrated that, by living in groups, animals reduce their vulnerability to predators. Percent time animals spent on the ground was indirect evidence for reduction in vulnerability to predators as a result of living in groups (but see van Schaik et al., 1983b; de Ruiter, in press). A better way to study effects of predators would be to look at the rate of predation in groups of different sizes and see whether there is any correlation between group size and the rate of predation (see Page and Whitacre, 1975).

This study supported Wrangham 's (1980) hypothesis that by living in groups, animals increase their feeding efficiencies. However, it has not rejected van Schaik's (1983) hypothesis that by living in groups, animals reduce their vulnerability to predators.

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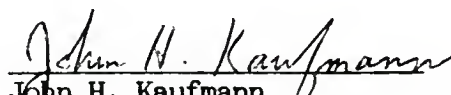
BIOGRAPHICAL SKETCH

Sompoad Srikosamatara was born on June 16, 1955, in the
province of Nakhorn Srithammarat, Southern Thailand. He grew up
and received his primary education in a small town, Ban Pong,
Ratburi which is about 80 Km south of Bangkok. Before he
attended a university, he spent 2 years in a high school, Triam
Udom Suksa School. He received both his B.S. degree in biology
and M.S. degree in environmental biology at the Mahidol
University.

During his senior year at the Mahidol University, he read
The Shadow of Man written by Jane Goodall and it made him decide
to do field work on primate behavior instead of biochemistry. He
did the first study on the ecology and behavior of the pileated
gibbon (Hylobates pileatus), an endangered species, in southeast
Thailand for his M.S. thesis. The work on the gibbons brought
him to a meeting in India where he met Dr. Robinson and Dr.
Eisenberg at the first time. That meeting was the first contact
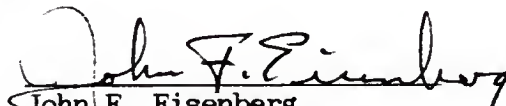that brought him to the University of Florida.

I certify that I have read this study and that in my opinion
it conforms to acceptable standards of scholarly presentation and
is fully adequate, in scope and quality, as a dissertation for
the degree of Doctor of Philosophy.

John G. Robinson, Chairman
Associate Professor of Zoology

I certify that I have read this study and that in my opinion
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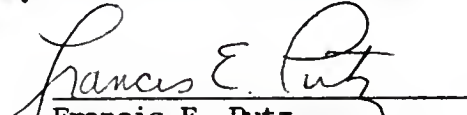
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I certify that I have read this study and that in my opinion
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This dissertation was submitted to the Graduate Faculty of the
Department of Zoology in the College of Liberal Arts and Sciences
and to the Graduate School and was accepted as partial
fulfillment of the requirements for the degree of Doctor of
Philosophy.

May, 1987   _____
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